

MORPHOLOGY AND RELATIONSHIPS OF THE HOLOCEPHALI WITH SPECIAL REFERENCE TO THE VENOUS SYSTEM

BARBARA J. STAHL¹

CONTENTS

Introduction	141	Discussion of Phylogenetic Clues from Other	
Materials and Methods	143	Organ Systems	162
Description of the Venous System	144	The Nervous System	162
The Subcutaneous Veins	145	The Skeletal System	167
The Deep Veins		The Muscular System	176
Precardiac Group	147	The Urogenital System	181
Postcardiac Group	151	The Digestive System	186
The Hepatic Portal System	154	Conclusion	190
Discussion of the Significance of the Circula-		Acknowledgments	193
tory System to the Problem of Holoce-		References Cited	193
phalian Relationships	155		

INTRODUCTION

Although the evolutionary relationships of the Holocephali have been under consideration for years, no one theory of their descent has appeared so satisfactory that the question may be laid to rest. This paper is the result of the continuing search for progress in clarifying the position of these fishes. To this end an investigation of the venous system of *Chimaera coliei* Lay and Bennett (*Hydrolagus coliei*) has been undertaken, and a reassessment of the anatomy of the Holocephali has been made, taking into consideration both the structural arrangements revealed by the new dissection and current paleontological knowledge.

The problem of classifying the holocephalian fishes (the living genera of which are: *Chimaera*, *Callorhynchus*, *Rhinochimaera*, and *Harriotta*) has become more and more difficult as the understanding of

the history of fishes has grown. In contrast to Linnaeus who set the Holocephali down in the same group with the sharks, rays, sturgeons, and lampreys because of their cartilaginous skeleton, modern scholars are giving much thought to the propriety of even including them with the elasmobranchs.

The day has passed, too, when an investigator could seek to solve the problem by focussing upon a single structure and suggesting that it indicates a probable evolutionary relationship. This point bears mention because the spotting of isolated similarities has generated several hypotheses, concerning the evolution of the Holocephali, which have proven untenable when an intensive examination is pressed. Based upon reasoning of this sort is the idea that the Holocephali might possibly be allied to the lungfishes through the common possession of autostyly and cutting toothplates. When the idea was tested by further study, it was

¹ St. Anselm College, Manchester, N.H.

shown that the nature of the palatoquadrate fusion was different, that the toothplates were surely not homologous structures, and that other anatomical characteristics were not alike. When paleontological evidence is considered, the probability of a relationship between the Holocephali and Dipnoi recedes still further. Despite the large amount of cartilage in the skeleton, lungfishes have definitely sprung from ancestral bony fishes, which sets them far from the holocephalians. The latter fishes arose probably from forms more nearly, though not necessarily very closely, allied with the ancestors of sharks than with the predecessors of the Osteichthyes. Assuming the truth of this statement, one can cast aside the hypotheses which link the Holocephali to fishes like *Latimeria* and *Polypterus* whose position as bony fish is well established, and also those which embed the holocephalians in the line of fishes leading to tetrapods.

Currently only two possibilities of holocephalian origin are receiving serious attention. One opinion holds that holocephalians are aberrant off-shoots from ancient cartilaginous fishes. Specifically, this school favors the idea that the Holocephali are descendants of the bradyodonts, an extinct group of presumed shark relatives distinguished by nonreplaceable teeth of a peculiar histological structure. Although no wealth of fossil material exists, paleontologists have speculated that at least some of the bradyodonts were autostylic, as are the Holocephali. A leading advocate of the bradyodont origin of the Holocephali, Moy-Thomas (1936) has studied one of the rare bradyodont fossils which consist of more than teeth and spines and found in it many resemblances to holocephalian design. This specimen, the cochlodont *Helodus simplex*, dates from Carboniferous times. If it is ancestral to the Jurassic chimaerids, one must assume that all the distinctive holocephalian characteristics which *Helodus* does not possess were evolved in the intervening years. Other bradyodonts such as

Menaspis and *Oracanthus* have been discussed in relationship to the problems of holocephalian origin, but they have either possessed structures like the spines on the head of the former which makes one hesitate to place them in the direct ancestral line or they have been, like the latter, in too fragmentary a condition to allow a thorough comparison. In a recent paper, Patterson (1965) concludes that the bradyodonts are closely enough related to the Holocephali to be grouped with them in the class Holocephali, but abandons the idea that *Helodus* or any other bradyodont is ancestral to the holocephalian line.

The second possible source of the Holocephali is an older one. Amongst the ptyctodonts, a placoderm group, have been found several fossil forms that show characteristics which could be ancestral to those of holocephalians. The resemblances were recognized early (Pander, 1858), but neglected after the ptyctodonts were allied with the arthrodire, and after Moy-Thomas offered, in *Helodus*, a bradyodont ancestor for the holocephalians which had long been classified in a general category with sharks. The idea of a ptyctodont ancestor has returned to favor, however, as the magnitude of the differences between holocephalians and sharks has been revealed. It seems now most attractive to find a stock, traceable far back into the Devonian, which could be ancestral to the Holocephali. There are a number of fossils (in a more complete state than many of the cochlodont forms) which have been used as a basis for comparison with extinct and Recent chimaerids. Of these forms, students of holocephalian evolution cite most often *Rhamphodopsis*, *Ptyctodus*, and *Ctenurella*. The last is considered by Ørvig (1962) to show a remarkable number of similarities to the Holocephali. However, the ptyctodont-holocephalian relationship, while possible, is far from proved. There are still serious questions to be solved. One must suppose, for instance, if the relationship is a fact, that over the countless generations which

separated the Devonian ptyctodonts from the Jurassic chimaerids the animals lost their distinctive pattern of dermal armor, their pectoral spines, and their internal bone. While changes of this nature are not impossible, there is no fossil evidence to prove that they did take place.

In trying to decide whether it is more likely that holocephalians originated from ptyctodonts than from a group closer to the shark line, one turns normally to the data available from embryological studies. In the case of the Holocephali, very little embryological work has been done. Since the holocephalian fishes lay their eggs, already fertilized and enclosed in a case, in deep water, the embryos are not often obtained. There have been only two studies made of embryonic forms: that of Schauinsland on *Callorhynchus* (1903) and that of Dean on *Chimaera* (1906). Although both studies were elegant pieces of work, a lack of certain stages resulted in the absence of observations of the fusion of the upper jaw and the step-by-step formation of the hyoid arch, for example. An understanding of these two points would shed great light upon the evolutionary question.

Besides the paleontological and embryological approaches, there is a third useful avenue of investigation. The contribution from the area of comparative anatomy cannot be omitted in assembling evidence which bears upon the problem. Although holocephalian fishes have been dissected numerous times, the work upon the anatomy of these fishes is not completed. In early anatomical investigations the dissector often placed his emphasis upon structures which are not the best keys to the evolutionary problem. There is no information available concerning some of the areas which are of great interest from the comparative point of view.

One such area, that of the venous system, has been completely untouched. Although there have been publications concerning the distinctive portions of the arterial pathway, there is nothing in the literature about

the pattern of vessels returning blood to the heart. It was in the hope that the venous system would show special features which might serve as clues to a better understanding of holocephalian evolution that this study was undertaken.

MATERIALS AND METHODS

Since it was desirable to avoid describing as the general occurrence an anomalous vessel in a single fish, dissections were repeated until it appeared certain that a particular pattern was a normal and not an abnormal feature. The relatively large number of specimens available made this method possible. The first specimen to be dissected was a female *Chimaera colliciei*, uninjected, which had been preserved in formalin and transferred to alcohol. A group of twelve specimens of *Chimaera colliciei* were obtained fresh-frozen from Vancouver, B. C., through the kindness of Dr. Norman J. Wilimovsky. The procedure used with these animals was to defrost them, inject immediately with latex, preserve first in formalin, and after five days to transfer them in several steps to 70 per cent alcohol. The last six specimens of *Chimaera colliciei*, four females and two males, were received already injected with latex through the kind efforts of Dr. Richard Snyder. For comparative purposes one specimen of *Callorhynchus* and one specimen of *Rhinochimaera* were examined.

Several methods of injection were tried. Because of the delicate nature of the vein-walls and the consequent similarity between veins and strands of connective tissue in some areas, nothing was interpreted as a vein unless it was observed filled with an injecting material or remnants of brown-colored agglutinated blood. In the first uninjected specimen described above, a carmine suspension was injected in area after area as the dissection proceeded. India ink was also tried. In the defrosted specimens, as noted, latex was used. Finally, to fill certain empty areas in the professionally injected specimens, ordinary poster paint

was employed in its regular concentration and also in a slightly diluted form.

All these media were introduced through a glass-barreled syringe fitted with a number 23 needle inserted into an inch-and-a-half-long piece of polyethylene tubing, size 50. The tubing was tied into the vessel through which the injection was made.

The routes that were available for injection were limited. Injection via a sinus proved impractical, because the injecting apparatus could not be tied tightly to the delicate sinus-wall. Very fine veins disintegrated under the most careful handling. Only large veins of well-defined cylindrical shape were useful. Injecting through them was hampered only by the presence of valves which restricted the amount of injection material able to pass beyond into tributary vessels. In particular, this difficulty arose in getting material to pass from the common cardinal vein forward into the anterior cardinal sinus and also in filling the deep veins of the fins. Although various vessels were tried as the dissection advanced, for the initial attempt to fill as much of the venous system as possible, two veins were relied upon. To inject the hepatic portal system, the posterior dorsal intestinal vein was employed. To fill the systemic vessels, injection was made into the lateral cutaneous vein immediately posterior to the scapula. This vein could be uncovered easily over a considerable distance by removing the skin just below the lateral line. Injection was made through this vessel first in an anterior and then in a posterior direction.

DESCRIPTION OF THE VENOUS SYSTEM

The veins return blood to the two common cardinal vessels which lie medial to the anterior edge of the scapular process of the pectoral girdle and empty into the lateral corners of the sinus venosus. On either side, three veins meet at the point at which the last pharyngobranchial cartilage articulates with a facet of the scapula, to create the common cardinal of that side.

These three are the anterior cardinal, the posterior cardinal, and the lateral cutaneous veins. The first comes from a forward direction, the second comes from the posterior region, and the third runs downward and slightly caudad to meet the other two. Into the upper end of the common cardinal, the inferior jugular vein opens. More ventrally, the brachial sinus opens into the common cardinal from the posterior side (Pl. 5, B, C).

Each of the major venous trunks will be described with its tributaries and the areas which they drain. So that the description may be more easily understood, the pattern of the venous system is presented first in concise, outline, form:

- I. The Subcutaneous System
 - Lateral cutaneous vein
 - Caudal tributary
 - Axial tributaries
 - Pelvic anastomotic area
 - Clasper veins
 - Ventro-lateral tributary
 - Postscapular tributary
 - Dorso-lateral axial branch
 - Dorsal fin branch
 - Prescapular tributary
 - Dorsal cephalic branch
 - Anterior subcutaneous tributary
 - Ventral cephalic branch
 - Opercular branches
 - Subscapular tributary
- II. The Deep Veins
 - A. Precardiac vessels
 - Anterior cardinal sinus
 - Inferior jugular vein
 - Posterior cerebral vein
 - Postorbital vein
 - Hyoid tributary
 - Orbital sinus
 - Maxillo-facial vein
 - Preorbital branch
 - Deep labial branch
 - Orbito-nasal vein
 - Posterior palatal vein
 - Superior adductor mandibular vein
 - Anterior cerebral vein
 - Posterior cerebral tributary
 - Anterior cerebral tributary
 - Ethmoidal vein
 - B. Postcardiac vessels
 - Brachial sinus
 - Posterior brachial vein

- Anterior brachial vein
- Posterior cardinal sinus
 - Ventro-anterior parietal vein
 - Deep epaxial veins
 - Dorsal fin sinus
 - Medial dorsal vein
 - Anterior epaxial vein
 - Spino-basal vein
 - Esophageal veins
 - Anterior parietal veins
 - Veins of the reproductive tract
 - Renal veins
 - Femoral vein
 - Rectal tributary
 - Dorsal fin tributaries
 - Ventral fin tributaries
- Hepatic veins
- Renal portal veins
- Caudal vein
- Parietal veins
- Ventro-posterior parietal vein
- Hepatic portal vein
 - Intra-intestinal vein
 - Anterior dorsal intestinal tributaries
 - Anterior ventral intestinal vein
- Mesenteric vein
 - Dorsal posterior intestinal vein
 - Ventral posterior intestinal vein
 - Auxiliary splenic veins
 - Lieno-pancreatic vein
 - Auxiliary pancreatic veins

The subcutaneous system is shown in Plate 1. The deeper veins are represented diagrammatically in Plates 2 and 3.

THE SUBCUTANEOUS VEINS

There is an extensive system of subcutaneous drainage (Pl. 1). The vessels which form it lie in the loose connective tissue under the skin. Although their pathways vary somewhat in different specimens, the basic pattern of flow is generally the same. Assigning names to the vessels of this system is a hazardous business because of the numerous anastomotic connections which are present, but there are several principal trunks which can be specifically distinguished.

The chief collecting trunk deserves the name *lateral cutaneous vein*, for it courses anteriorly, paralleling the lateral line. In the caudal region it is located about a half inch below the lateral line canal, but at the

level of the base of the pelvic fin it bends dorsally somewhat and can be followed forward into the trunk region where it is to be found just ventral to the lateral line. At its anterior end it continues forward lateral to the muscle-covered dorsal extension of the scapular cartilage, bends medially around the anterior edge of this cartilage, and then runs ventrally for a short distance to form, with the anterior and posterior cardinals, the common cardinal vein. As it passes ventrally on the medial side of the scapula, it enlarges sufficiently to merit the name of *subscapular sinus*. Where it approaches the upper end of the common cardinal it is flanked by passing nerves, the anterior nerve trunk containing fibers of the cervical plexus which innervate the hypobranchial muscles, and the posterior trunk containing branches of the first through third spinal nerves. (There is also in the anterior trunk a small group of visceral vagus fibers.)

The lateral cutaneous vein, as the principal trunk of the subcutaneous system, has the firmest wall of any vein involved in the superficial drainage. The toughness of the wall is due primarily to an ensheathing layer of dense connective tissue. This vein receives many tributaries which will be described below, beginning with those bringing blood from the most posterior regions.

Although, in the caudal region, the lateral cutaneous runs forward a short distance ventral to the lateral line, there is another, smaller vein which accompanies the sensory canal. This *caudal tributary* turns ventrally to empty into the lateral cutaneous vein at the point along the length of the body which is on a level with the posterior limit of the pelvic fin attachment.

As the lateral cutaneous vein courses forward, it collects blood returning from the superficial regions of the axial musculature dorsal and ventral to it. The *axial tributaries* are arranged in an orderly but not a rigidly segmental pattern. The dorsal tributaries are relatively short and in the region of the trunk posterior to the dorsal fin spine have as their source a network of little veins

which forms a narrow band dorsal to the lateral line and parallel to it. The ventral tributaries collect blood from a much greater area and in the pelvic region are considerably enlarged. There, they draw from an anastomotic network of veins. As part of that network, a vein can be seen running along the line of origin of the superficial levator muscle of the fin. The location of this line may be described as being about halfway between the lateral line above and the base of the pelvic fin below. Into this vein run tributaries from the levator muscle, from the axial muscle medial to the levator, and from the axial muscles which are posterior and ventral to the pelvic region. These tributaries have connections, also, with two veins which together encircle the base of the fin. One runs around the base laterally; the other runs around it medially, thus edging the anal region. These two vessels receive veins draining the fin web and the superficial muscles of the fin itself. In the male *Chimaera*, the veins of the clasper, which receive blood from the erectile tissue in the clasper tips, become superficial as they course proximally and empty into the venous ring at the fin base (Pl. 4, A). The chief *clasper veins* are two which appear on the ventral side of the clasper. One drains each prong, and they merge shortly before emptying at the posterior edge of the fin base.

From the anterior corner of the venous network in the pelvic region there flows forward a vessel of rather large size which gathers blood from the skin and superficial axial musculature ventral to the field served by the axial tributaries to the lateral cutaneous vein. This vessel meanders forward over a slightly wavy pathway, finally curving dorsally behind the pectoral region to empty into the lateral cutaneous trunk just before the latter turns inward around the anterior edge of the scapula. The name *ventro-lateral tributary* seems appropriate for this vein. In one specimen which had been injected with India ink, small veins

were seen entering it from the posterior edge of the operculum dorsal to the gill opening and from the ventral part of the trunk immediately behind the opening from the gill chamber. The veins in this area were not injected successfully in any other specimen.

The lateral cutaneous trunk receives two sizable tributaries bearing blood from dorsal regions. The first one to be described begins lateral to the muscle-covered posterior tip of the scapular cartilage which is bound against the epaxial muscles at the base of the dorsal spine. This vein, called the *postscapular tributary*, receives blood from the *dorsal fin branch*, draining the web and muscles of the dorsal fin. Halfway along its course to the lateral cutaneous vein, the postscapular tributary receives the *dorso-lateral axial branch*. The latter vessel is a long one, running parallel but dorsal to the lateral cutaneous vein. It collects blood returning from the superficial epaxial muscles which lie dorsal to those drained by the axial tributaries of the main lateral trunk. Some of the branches which join the dorso-lateral axial branch can be seen to connect also with a median dorsal vessel whose blood flows eventually into the posterior cardinal sinus. These connections represent one of the few anastomoses between the subcutaneous and the deep venous drainage systems.

Far dorsally, near the base of the dorsal fin spine, there are prominent vessels which form an anastomosis between the postscapular vein and the second of the two sizable tributaries from the dorsal region. The second one, the *prescapular tributary*, courses ventrally just in front of the anterior edge of the scapula to join the lateral cutaneous vein at the point at which it turns medially to meet the common cardinal. Shortly before emptying into the lateral cutaneous, the prescapular tributary receives the *dorsal cephalic branch* carrying blood from the flattened triangular-shaped dorsal surface of the head. Atop the head, the dorsal cephalic branches of the left and

right sides are connected through anastomosing venules. As it runs toward its meeting with the prescapular, the dorsal cephalic follows the posterior portion of the supraorbital sensory canal, collecting blood from fine venules which parallel the mucous canals above the eye. A small vein draining the skin immediately above the orbit may empty into the dorsal cephalic branch or may be connected to the tributary next to be described.

This tributary, called the *anterior subcutaneous*, empties into the lateral cutaneous vein at the same point at which the prescapular enters it. Approaching that point, it courses dorso-posteriorly, approximately paralleling the posterior quarter of the suborbital sensory canal. This vessel receives several *opercular branches* (some of which may anastomose with the ventrolateral tributary near its anterior end). It receives also a *ventral cephalic branch* which drains veins collecting forward and ventral of the orbit and fine venules which parallel the group of mucous canals anterior and ventral to the eye. The ventral cephalic branch may also receive blood from the region just posterior to the lower jaw, but in no specimen could the injection medium be made to penetrate that far forward.

The last tributary to the lateral cutaneous vein which remains to be mentioned is the *subscapular*. This one is really a small sinus, lying against the medial surface of the scapular cartilage. It receives venules from the cartilage itself and from two fine veins which follow the posterior border of the cartilage, one coming from a ventral and the other from a dorsal direction. The subscapular tributary is the last one to join the lateral cutaneous vein before it empties into the common cardinal vein.

THE DEEP VEINS

Precardiac Group

The return of blood from the deep portion of the body anterior to the heart takes

place through the *anterior cardinal sinus*. This sinus is exposed by lifting the dorsal constrictor muscle which covers the gill area. As the connective tissue beneath the muscle is cleared away dorsal to the operculum, the scalpel falls into the sinus. The blood-space lies lateral to a muscle originating under the subocular shelf and inserting posteriorly upon the last pharyngobranchial cartilages. This muscle, the trapezius internus of Vetter (Vetter, 1878), covers a portion of the branchial branches of the vagus nerve. The latter are visible through the medial wall of the anterior cardinal sinus for a short part of their pathway ventral to the muscle-band. The sinus is situated dorso-laterally with respect to the efferent branchial arteries and entirely dorsal to the branchial skeleton.

Just as the anterior cardinal sinus, at its posterior end, curves slightly ventrad to join the common cardinal, it receives the *inferior jugular vein*. This vein, which enters the sinus from the ventral side, has so broad a mouth that it might be interpreted as opening partially into the common cardinal itself. The inferior jugular originates far anteriorly behind the lower jaw (Pl. 5, A). Although its main branch comes from within the hyoid "tongue" which protrudes from the floor of the mouth, branches also reach it from the thyroid gland, the ventro-medial fibers of the ventral constrictor muscle, and the anterior portion of the coracomandibularis. Veins from these sources were actually seen, but it is also possible that there exist venules which failed to be injected, draining all the tissues located posterior to the mid-ventral portion of the mandible.

About a centimeter behind the mandible, the inferior jugular vein turns medially and, running dorsal to the coracohyoideus muscle, almost meets its fellow of the opposite side. Without actually doing so, however, the vein turns posteriorly and takes a path lateral to the insertion points of the coracobranchial muscle fibers upon the branchial cartilages. The vein follows the coracobranchial insertion line, flaring widely from

the ventral midline and curving dorsally as it does. This route leads the inferior jugular to the postero-ventral corner of the anterior cardinal sinus as described above. In its course along the inserting border of the coracobranchial, it receives blood from the lateral and medial sides of that muscle-sheet.

The drainage of the coracomandibularis and coracohyoideus muscles is only partly accounted for by the inferior jugular vein. Although no other veins in this area were injected, dissections suggest that there may be a deep vein immediately ventral to the ventral aorta which provides additional drainage (Pl. 4, B). From it blood may return through small veins in the dorsal pericardial wall to the common cardinal or possibly over a more ventral course to a pair of veins, to be described below, which run through a channel in each side of the pectoral girdle.

Farther forward than the entry-point of the inferior jugular the anterior cardinal sinus receives into its dorsal side the *posterior cerebral vein* (Pl. 6, A). This vessel collects blood from fine veins over the cerebellum and from membranes in the dorsal part of the cranial cavity. Since there is little likelihood, from the position of this vein, that it returns blood from any part of the cerebrum of *Chimaera*, the use of the term "cerebral" in naming the vessel is technically incorrect. The adjective has been retained merely as a convenience to indicate that this vessel is the posterior of two draining the brain region. There is a possibility that fine veins which connect with the posterior cerebral may also connect with the orbital sinus via an anastomosing vein that passes through the wall of the orbit with the trochlear nerve. The existence of a vein traveling with that nerve was not clearly demonstrable, however, and so is best left in question.

The posterior cerebral vein is formed as a median vessel in the dorsal portion of the cranial cavity over the medulla oblongata between the endolymphatic ducts. In

addition to the blood from the brain and associated membranes, the posterior cerebral receives tributaries from the inner ear of each side. These veins pass through the wide opening by which the cavity of the inner ear communicates with that of the brain and hence do not pierce cartilage. Immediately posterior to the point of its formation, by the confluence of the small vessels described, the posterior cerebral vein widens, over the rear part of the medulla, to form a small sinus. Into the posterior end of this sinus run several little tributaries carrying blood forward from the spinal cord. The blood collected in the sinus leaves it through two veins which may be considered as paired posterior cerebrals, continuing from the median vessel. Each passes directly into a long, ventrally directed channel in the cartilage on its own side of the chondrocranium. Each channel, occupied solely by the paired portion of the posterior cerebral vein, terminates by passing dorsal to the vagus nerve (which is also traversing the cartilage at that point) and opening ventro-laterally, anterior to the foramen of the latter. The posterior cerebral vein runs forward close under the otic region of the chondrocranium and then turns laterally at the level of the posterior limit of the semicircular canals to join the anterior cardinal sinus.

At the anterior end of the anterior cardinal sinus, lies the opening of the *postorbital vein* (Pl. 6, A). This vein, which travels through the posterior wall of the subocular shelf, in a ventral direction, with the hyomandibular branch of the seventh nerve, forms a bridge between the orbital sinus and the anterior cardinal. As it enters the latter, dorsal nutrient veins from the gill septa were seen, in one specimen, to send a common stem dorsally to this blood channel. In no other specimen were these little veins detected.

The postorbital vein was examined with care, for it was expected that the hyoid sinus should open into it or nearby. However, no evidence was found in any speci-

men of the existence of a shark-like hyoid sinus. There was only a small vein, the *hyoid tributary* (Pl. 7, B), which could be traced ventrally to the dorsal tip of the ceratohyal cartilage and no further as a dissectable vessel. Posterior to the ceratohyal cartilage and anterior to the afferent branchial artery, in the position of the selachian hyoid sinus, it was possible to trace an uninjected vein in specimens with a favorable distribution of agglutinated blood. Although a connection with the above-described small vein was not clearly seen, it is possible that there was one and that this entire blood pathway is homologous to the selachian hyoid vessel.

In each dissection of the region ventro-anterior to the postorbital vein, the subocular shelf and the cartilaginous bar which runs to the mandibular articulation were removed after examination of the bordering tissues. Beneath the cartilage and immediately dorsal to the skin of the roof of the mouth was a layer of loose connective tissue. The veins running through it were visible only when they remained filled with blood, as the injection mass never penetrated to them. They anastomosed with each other and one ran to join the postorbital as it emerged from beneath the subocular shelf (Pl. 7, B). It seems possible that the vessel traced from the postorbital vein to the tip of the ceratohyal may have connections with the veins of the connective tissue layer via a fine vessel which passes forward, dorsal to the ceratohyal, in company with the efferent pseudobranchial artery. This artery passes dorsally, pierces the chondrocranium, and splits into the cerebral and optic arteries. (In its dorsal course it runs along the posterior edge of the lymphomyeloid mass [Kolmer, 1923] dorsal to the skin of the palate.) Although it is difficult to discern, it is probable that a vein travels with the artery. Judging from the pathway of the artery, this vein might have connections to the network of veins in the connective tissue just described and to the orbital sinus as well. It is also

possible that some drainage from the base of the brain might be carried to the orbital sinus or to the postorbital vein via the pathways which exist through the connective tissue.

The *orbital sinus* receives all the blood returning from the head except that which passes through the subcutaneous vessels, the inferior jugular, and the posterior cerebral veins. The sinus encircles the orbit medial to the nerves running through it. Intimately connected with this sinus is lymphomyeloid tissue. This tissue, which seems to be situated in the lateral edges of the blood-space, is present in such quantity at the ventro-anterior corner of the orbit that it bulges laterally in two sizable masses which are visible as soon as the skin is removed from that area. When the skin, connective tissues, and mucous canals¹ are removed from the head in front of and below the orbit, the largest tributary to the orbital sinus can be seen. This vessel, the *maxillo-facial vein*, coursing dorsally over the posterior palatoquadrate region and up over the subocular shelf, enters the ventral side of the orbital sinus anterior to the point at which the postorbital vein leaves it (Pl. 6, A). As the maxillo-facial vein approaches the sinus it assumes a position medial to the nerves which run out of the orbit. The vein carries blood from the deep portions of the overlying mucous canals, from the dermis of the upper lip and the area above it lateral to the labial cartilages, and from the muscles of the facial region which insert upon the labial cartilages and the lower jaw. As the maxillo-facial vein approaches the orbital sinus, it is joined by the *pre-orbital branch*, draining the muscle tissue anterior to the eye, and by small veins

¹ In the head region of *Chimaera* there are two groups of tubules lying under the skin which exude mucus through pores at their posterior ends. The dorsal set of six parallel tubules lies above the orbit and extends behind it. The ventral tubules, approximately the same in number and arrangement, cover an area of the face ventral to the eye and anterior to it.

which come from tissues lying just posterior to the maxillo-facial vein itself.

Since the maxillo-facial vein was nearly empty of blood in the frozen-and-thawed specimens and did not prove amenable to injection, its anatomy was studied in the fish which had been injected with latex and preserved immediately in formalin. In these animals the maxillo-facial vein was observed only upon the left side. The right side showed what appeared to be a large sub-surface pool of agglutinated blood—surely an artifact. Since the veins on the left were entirely empty, it is probable that the fresh-caught fish were stored right-side-downward, causing the blood to accumulate and to obliterate the vessels on that side. Although the vessels of the left side of the face were not filled with latex, it was possible to trace them by injecting poster-paint into the orbital sinus and expressing it into the facial veins by pressing gently upon the eye.

A small *deep labial branch* of the maxillo-facial vein brings blood from the lower lip and jaw, the upper jaw region medial to the labial cartilages, and the nasal capsule (Pl. 7, A).

There are two other veins which enter the orbital sinus from the ventral side, but both of them pierce the subocular cartilage to do it. The *orbito-nasal vein* passes through its own foramen. As it travels toward the foramen from the nasal region, it lies against the dorsal surface of the suprapalatal lymphomyeloid mass. Tracing this vein anteriorly, one finds that it can no longer be separated from the lymphomyeloid tissue where the anterior tip of the mass abuts the posterior side of the nasal capsule.

The second vein which reaches the orbital sinus by piercing the subocular shelf has already been mentioned. This is the vessel which accompanies the efferent pseudobranchial artery along the posterior edge of the lymphomyeloid mass and thence through its subocular foramen. The vein has been called the *posterior palatal vein*

because its course lies over that area. Its relation to the suprapalatal lymphomyeloid tissue suggests that it plays a part in draining it. This vessel is never filled with the injection mass. Its presence is demonstrable only because of the blood left in it.

There are also veins which enter the orbital sinus in its antero-dorsal corner. To reach the orbital sinus at this point, the veins must traverse the posterior part of the ethmoid canal. The canal is a large, cartilage-roofed, median space dorsal to the portion of the cranial cavity occupied by the elongated telencephalon. It is separated from the brain cavity by a cartilaginous partition. The ethmoid canal, which is filled with lymphomyeloid material, encloses the ophthalmic nerves as they pass from the orbital region towards the snout. One of the veins which passes through the ethmoid canal on its way to the orbital sinus is the small *superior adductor mandibular vein*. It drains the most dorsal portion of the deep adductor muscle. Leaving the muscle, the vein passes inward through the wall of the ethmoid canal and joins the path of the superficial ophthalmic trunk, traveling with it through its foramen into the orbit.

A second vein, the *anterior cerebral*, enters the orbital sinus by passing through a foramen in the cartilage between the back of the ethmoid canal and the front edge of the orbit (Pl. 5, D). The foramen, which is medial to the departure-point of the ophthalmic profundus from the orbit, transmits only this vessel. The anterior cerebral vein brings blood back from the anterior end of the brain. It is formed as a median vessel within the cranial cavity by the union of a *posterior* and an *anterior cerebral tributary*. The posterior tributary runs from the tip of the long epiphysis (which extends forward to a position above the interorbital area) ventrad in a course which follows the curving posterior edge of the interorbital septum. The anterior cerebral tributary, which drains the telencephalic lobes, follows a dorsal pathway posteriorly

through the cranial cavity to meet the posterior tributary just below the ventral edge of the interorbital septum. The anterior cerebral vein produced by the union of the two tributaries passes antero-dorsally through the edge of the interorbital partition and then through a short channel in the cartilage to enter the posterior end of the ethmoid canal. There it bifurcates. Each branch turns posteriorly to enter the orbital sinus on its own side. Just before it leaves the ethmoidal canal each portion of the bifurcated anterior cerebral vein receives an *ethmoidal vein*. The ethmoidal veins bring blood back through the ethmoid canal from the most rostral part of the snout. These vessels enter the anterior end of the canal through the same pair of foramina through which the superficial ophthalmic nerves issue.

THE DEEP VEINS

Postcardiac Group

Ventral to the confluence of the anterior cardinal, lateral cutaneous, and posterior cardinal trunks, there is an opening into the posterior side of the common cardinal vein from the *brachial sinus*. That sinus, which receives all the blood returning from the pectoral fin, lies behind the base of the fin in the angle between it and the body wall. There is an extension of the sinus ventrally along the posterior side of the pectoral girdle which meets its pair in the midline. The entrance of the brachial sinus into the common cardinal is edged by a sharp fold which acts as a valve. It is this valve, apparently, which prevents good injection of the pectoral veins.

The brachial sinus receives blood from two sources. The larger contributor is the *posterior brachial vein*. It borders the posterior edge of the muscle mass of the fin. In dorsal view it can be seen running along the posterior side of a deep levator of the fin (Pl. 5, B). Although neither Vetter (1878) nor Shann (1919) gives a specific name to this muscle, it can be

recognized easily through its origin from the postero-medial surface of the scapula, its strap-like shape, and its insertion upon the metapterygial cartilage. The brachial nerves run from the body wall through the axial region toward the posterior brachial vein. Upon reaching it, they divide into dorsal and ventral branches, the former passing over the vein and the latter under it. The posterior brachial vein receives blood from the deep portions of the posterior half of the pectoral fin.

The second source of the blood collected by each brachial sinus is the *anterior brachial vein*. This vein emerges from a channel in the cartilage of the pectoral girdle to pour its contents into the sinus. The channel, which for most of its length contains the brachial artery as well as the anterior brachial vein, is a long one, piercing the cartilage in the coracoid region at a point close to the ventral midline and running dorsally through the girdle to open on the medial edge of the scapular process near the brachial sinus. Between its beginning in the coracoid area and its termination adjacent to the sinus, the channel opens to the surface twice more: there is a foramen facing ventro-laterally anterior to the articulation of the fin and another facing posteriorly dorsal to the base of the fin. Although the most ventral opening of the channel is sizable and set in the anterior side of the coracoid bar, no veins could be seen entering it from the coracomandibular muscle which originates from that surface of the girdle. Since the veins draining the muscle fibers in that area remained uninjected in every specimen, it is possible that such veins do exist but were not observed.

Between the entrance to the channel in the coracoid area and the ventro-lateral foramen mentioned above, the channel is filled with lymphomyeloid tissue like that in the head region. If the passage does carry a vein from the area of the hypobranchial musculature, the vessel would undoubtedly have connections with the

vascular network of the lymphomyeloid substance. The first vein which appears certainly in the channel, however, is the tributary draining the deep, anterior ventral part of the fin. This vessel enters the passage through the ventro-lateral opening and follows the path of the channel dorsad. A tributary from the deep part of the anterior dorsal half of the fin enters the channel next, through the posterior foramen, and merges with the tributary from the ventral part of the fin to form the anterior brachial vein. It is this vein which leaves the channel at its dorsal termination to enter the brachial sinus.

Of the major trunks which empty into the common cardinal vein, the only one which remains to be described is the *posterior cardinal sinus*. Although this vessel is paired, there are numerous, sizable communications between the left and right sides, and posteriorly, at the origin of the trunk between the kidneys, there is a single median portion. There are four constant features concerning the anterior portion of this sinus which should be noted. Firstly, the entrance into the common cardinal of each side is cavernous. An injection mass introduced into the lateral cutaneous vein always descends and turns posteriorly into the posterior cardinal sinus rather than entering the smaller opening of the anterior cardinal. Just as the sinus approaches the common cardinal, the subclavian artery and two spinal nerve branches cross through it. Secondly, there seems to be a connection between the posterior cardinal and the brachial sinus. The connecting passage runs from the ventro-lateral edge of the posterior cardinal to the brachial sinus dorsal and posterior to its opening into the common cardinal. Thirdly, the left and right posterior cardinal sinuses extend ventro-laterally to meet each other in the ventral midline. This midline communication parallels that of the brachial sinuses and is separated from it by a sheet of connective tissue. It is to this part of the posterior cardinal sinus that the left and

right *ventro-anterior parietal veins* bring blood from the deep anterior ventral and anterior ventro-lateral axial musculature. Fourthly, the sinus of each side extends dorso-medially as a blind pouch forward of its point of union with the anterior cardinal sinus. Thus, a cross-section made just in front of the anterior edge of the scapula shows the left and right pouches close to the midline above the branchial region and the anterior cardinal sinus of each side lying in a more ventro-lateral position.

Since the posterior cardinal sinus runs retroperitoneally against the dorsal body wall between the dorsal aorta and the more laterally placed kidney, the veins from the deep epaxial muscles surely empty into it. These fine *deep epaxial veins* were not injected and so remained invisible, but their presence may be predicated with safety.

Besides this drainage and that from superficial regions of the dorsal musculature via the subcutaneous system, there is one other route to be mentioned: between the left and right epaxial muscle groups in the trunk region can be found a *median dorsal vein* (Pl. 6, B). This vessel was injected successfully and seen to collect from the most dorsal parts of the musculature. Anastomoses existed between its tributary veins and those of the subcutaneous system. The median dorsal vein carries its blood forward to a median *dorsal fin sinus* set behind the base of the dorsal fin. This sinus has a single anterior opening on each side through which blood leaves it. These openings lead to the posterior cardinal sinuses. The blood returned from the median sinus by this route enters the posterior cardinal far forward, flowing into the blind pouch which extends anteriorly and dorsomedially into the anterior tip of the coelom.

Posterior to the opening of this sinus, on a line with the base of the dorsal spine, an *anterior epaxial vein* enters the posterior cardinal on each side, bearing blood from

deep muscles forward of the dorsal fin. Medial to its point of entry is the cartilage plate which supports the dorsal spine. Against the side of this plate runs a vessel, the *spino-basal vein*, which connects the subcutaneous veins at the base of the fin-spine with the posterior cardinal sinus deep below.

The remaining tributaries to the posterior cardinal enter it more ventrally. There are several which come from the esophageal wall, leaving it as the gut tube makes its entry into the anterior end of the body cavity. In the region of the trunk anterior to the kidneys, *anterior parietal veins* on each side contribute blood from the most dorsal portions of the hypaxial musculature. The gonads and the ducts of the reproductive tract send their blood to the posterior cardinal, too. The blood from these structures seems to collect in sinuses between the double walls of the suspending dorsal mesentery. The sinus paralleling the oviduct of the mature female is quite spacious. There are veins running medially from it over the short distance to the posterior cardinal sinus. Around the anterior end of the functional kidney there is a wider communication between the two sinuses. The male fishes available for dissection were small and apparently not fully mature. The vas deferens was very fine and bound closely to the lateral border of the gland of Leydig (the transformed anterior end of the kidney). The venous drainage of the duct was invisible.

The *renal veins* run their usual short course, leaving the kidneys ventro-medially and entering the posterior cardinal sinus. Posterior to the entrance of all but a few of the renal veins the posterior cardinal sinus in *Chimaera* receives a vein which does not usually empty into it in cartilaginous fishes. That vessel, the large, firm-walled *femoral vein* (Pl. 7, C), is situated posterior to the femoral artery and, at the fin-base, is formed from *dorsal* and *ventral fin tributaries*, branches which come from the deep dorsal and ventral surfaces of the fin. Al-

though the femoral vein is strong enough to withstand the injecting process, it proved impractical to use it as a route for injecting the deep veins of the pelvic fin because of a valve at its distal end which prevents backflow.

A short distance proximal to the fin-base, the femoral vein receives the *rectal tributary*. This vessel collects blood from a capillary network in the wall of the rectum and also, in the female, from the problematical glandular "seminal receptacle."

As the femoral vein runs toward the posterior cardinal sinus it passes the lateral edge of the kidney and turns ventral to it. There is, however, a small branch which leaves the femoral, passes over the lateral edge of the kidney to the dorsal side and connects with the renal portal vein. The connection, the iliac vein (Pl. 3), is a delicate one and possibly not uniformly present. Because of the small size of the vessel its functional significance is doubtful.

The last contributor to the posterior cardinal sinus is a strange one for any vertebrate. Without a doubt, the *hepatic veins* (Pl. 9, A and B) empty into this dorsal channel instead of passing forward through the transverse septum to enter the sinus venosus. Inspection of the posterior wall of the sinus venosus showed a pair of openings so reduced as to be incapable of carrying the entire blood-flow from the liver. When the liver was cut transversely through the small area which is bound to the back of the transverse septum, there were no sinuses to be seen in the interior of the tissue. In *Chimaera*, however, the anterior attachment of the liver to the back of the transverse septum is not the only bridge between that gland and surrounding tissues across which a hepatic vein might travel. The front portion of each lobe is attached dorsally to the underside of the posterior cardinal sinus and thus to the roof of the coelom. The line of attachment extends along the dorsal edge of the right lobe of the liver for about a third of its length and along that of the shorter left lobe for half

of its length. When these areas of attachment were explored, it was found that hepatic veins of varying sizes passed through them, carrying blood from the liver directly to the posterior cardinal sinuses. The largest of these veins was one which drained the posterior two-thirds of the right lobe and entered the right posterior cardinal at a point immediately anterior to a mesentery strap extending from the midline, between the sinuses, to the tip of the pancreas. If the sinus wall is cut and deflected at that point, the dissector can look through a fenestrated membrane separating the sinus from the interior of the hepatic vein. This is the largest of all the hepatic veins and drains the entire free end of the large right lobe of the liver. For the most part, the branches feeding this hepatic vein lie dorsal to those from the hepatic portal vein which carry blood into the right lobe. Anterior to the point at which this large hepatic vein enters the posterior cardinal sinus, smaller hepatic veins enter the sinus separately. Although the left lobe of the liver is smaller, it is similarly drained. There are two main hepatic veins that leave it to enter the posterior cardinal sinus on the left side.

To conclude the description of the systematic venous drainage, one turns to the *renal portal veins* (Pl. 8, A). The blood entering the kidneys from the renal portal veins comes largely from the deep portions of the axial musculature. The muscles of the tail region send blood to the *caudal vein* which bifurcates behind the body cavity to become the left and right renal portal veins. These run forward along the dorsal surface of each kidney, medial to the mesonephric duct. At segmental intervals the renal portals receive veins from the body wall. The renal portals extend far forward, even beyond the region of the functional kidney, collecting the segmental *parietal veins* and finally dwindling to nothing about a centimeter behind the pectoral fin. At the level of the anterior edge of the pelvic girdle the renal portal receives

the *ventro-posterior parietal vein*. This vessel can be seen through the peritoneum, lying parallel to the long axis of the body. It begins in the middle region of the trunk and carries blood posteriorly from the deep hypaxial muscles. Immediately anterior to the pelvic girdle it curves dorsally to join the renal portal. The only tributaries to the renal portal which do not return blood from axial musculature are the small veins from the posterior end of the mesovarium. For a short distance beyond the end of the oviducal sinus in the crowded posterior part of the body cavity, these vessels from the lower end of the oviduct enter segmental parietal veins as they are about to join the renal portal.

The Hepatic Portal System

Since the nature of the digestive tract and the arrangement in the body cavity of the associated glands are distinctive in chimaerid fishes, the pattern of the veins draining the system is also singular. Before trying to visualize the path of the vessels, one must understand several anatomical points. Firstly, there is no stomach in these animals. Instead of a long J-shaped structure there is a short continuation of the esophagus which reaches the beginning of the spiral intestine. Secondly, the spleen is not attached to the gut tube by mesenteries. The mesenteries are exceedingly reduced and the spleen is fairly free, bound only to the posterior end of the pancreas. When a fresh fish is opened, the pancreas and spleen appear to lie ventrally in the body cavity. Because the spleen has no relation to a stomach, the term "gastro-splenic" or "lieno-gastric" is not applicable to any vessel in the hepatic portal system. It is well to keep these facts in mind when pondering possible homologies between the vessels of chimaerid fishes and any others.

The *hepatic portal vein* is formed against the surface of the liver posterior to the base of the gall bladder by the confluence of the intra-intestinal, the anterior ventral intestinal, and the mesenteric veins (Pl. 8, B).

It runs immediately into the right lobe of the liver in one direction and, in the other, sends a large division along the posterior edge of the midventral portion of the liver. The blood carried in this vessel is distributed to the left lobe of the liver.

The first of the vessels which deliver blood to the hepatic portal, the *intra-intestinal vein*, drains the spiral valve and, as it emerges from the intestine wall, receives *anterior dorsal intestinal tributaries*. These vessels collect blood not only from the anterior wall of the spiral intestine but also from the posterior region of the esophagus which connects with it. These tributaries anastomose with others which converge to form the *anterior ventral intestinal vein* (Pl. 10, A). The intra-intestinal and the anterior ventral intestinal leave the intestine wall from points lying close against opposite sides of the bile duct. Running closely apposed to the duct, these vessels finally reach the hepatic portal vein.

The last of the vessels which contribute blood to the hepatic portal, the *mesenteric vein*, is formed by the confluence of the two posterior intestinal veins. The *posterior dorsal intestinal vein*, which drains the lower end of the intestine as far as the beginning of the rectum, receives tributaries which can be seen on the surface of the intestine wall. These tributaries anastomose with others which converge on the opposite side of the intestine to form the *posterior ventral intestinal vein* (Pl. 10, A). Both posterior intestinal veins leave the surface of the intestine to run free to a position against the side of the pancreas where they merge and are bound down. In their free portions, the dorsal and ventral veins have a different appearance: the ventral one is narrower and runs through a band of mesentery; the dorsal one is very wide in diameter and absolutely unconfined. At the point at which they merge and are tied to the pancreas, there is a thin mesentery strap which leaves to reach the dorsal midline behind the dorsal attachment of the liver.

The mesenteric vein, thus formed, receives several *auxiliary splenic veins* (the spleen is tied to the posterior end of the pancreas just behind the point where the two intestinals reach it) and then receives the relatively large *lienopancreatic vein*. The latter vessel travels through the length of the spleen and the portion of the pancreas which lies posterior to the origin of the mesenteric. After receiving the lienopancreatic vein, the mesenteric turns anteriorly and runs in company with the pancreatico-splenic artery, collecting from *auxiliary pancreatic veins* in its course. The mesenteric enters the hepatic portal in conjunction with the intra-intestinal vein (Pl. 10, B).

Additional Observations

One specimen of *Callorhynchus*, a small female, was examined after the dissections of *Chimaera collici* were completed. It was found that the pattern of the confluence of the major venous trunks to form the common cardinal agreed with the findings in *Chimaera*. The hepatic veins were also found to enter the posterior cardinal sinus. An inspection of the posterior wall of the sinus venosus showed extremely small apertures that were similar to the reduced hepatic openings in *Chimaera*.

DISCUSSION OF THE SIGNIFICANCE OF THE CIRCULATORY SYSTEM TO THE PROBLEM OF HOLOCEPHALIAN RELATIONSHIPS

The venous system of the chimaerids bears a greater resemblance to that of sharks both in the structure of its vessels and their arrangement than it does to the system of any other group of extant fishes. There are certain deviations from the selachian plan, however, which are certainly clues to the separate evolution of the holocephalian line. A consideration of the significance of the venous system to the question of holocephalian relationships necessitates first, recognition of the resem-

blances, and then evaluation of the differences which exist.

The veins in both groups of animals, like those of all fishes, possess little muscular tissue. Their walls are therefore exceedingly delicate and difficult to differentiate from connective tissue in gross dissection. Even the main vessels may be opened by a chance touch of a scalpel tip. It is the combination of fragile walls and the presence of valves which gives rise in both holocephalians and selachians to the difficulties experienced in injection procedures. The lack of detailed description of the drainage of the head region stems directly from the inability of investigators to introduce substances into the veins which empty into the orbital sinuses. The valves, which are mere folds of the lining of the vein wall, seem to have a like distribution in chimaerids and sharks if non-penetration of injection media can be taken as a guide to their location. The dissector can see that the entrance into the common cardinal from the anterior cardinal is valved but that the opening from the posterior cardinal is not. This arrangement is also shown for *Heptanchus* by Daniel (1934).

The main venous channels in holocephalians as in sharks are sinuses. In both types of fishes the largest ones are held together from within by a network of connective tissue trabeculae. The position of these sinuses relative to each other is not distinctive in the Holocephali.

A great part of the basic arrangement of the venous system of selachians is duplicated in *Chimaera coliei*. The orbital sinus is the major collecting point for blood returning from the tissues of the head. As in *Heptanchus*, *Mustelus*, and *Scyllium*, it receives the orbito-nasal and anterior cerebral veins. Although Daniel (1934), Parker (1886), and O'Donoghue (1914), who investigated the three sharks named, respectively, do not describe in detail the specific structures drained by the orbito-nasal vein, the vessel in *Chimaera* is probably exactly comparable except that it receives blood

from the palatal lymphomyeloid mass which the sharks do not possess. The anterior cerebral vein of *Chimaera* drains the same regions of the brain as the selachian vessel, although there is no reception of an ethmoidal vein in sharks, which lack an ethmoidal canal. The dissection of *Chimaera* revealed a maxillo-facial vein and two smaller vessels which also empty into the orbital sinus. That there are no comparable vessels shown for sharks is probably due to their having been uninjected and unreported rather than to their absence.

A postorbital channel exists in both holocephalians and sharks to carry blood from the orbital sinus to the anterior cardinal. Although its location relative to the two blood spaces it connects is the same in both types of fishes, its associations with skeletal and nervous elements are not identical. In *Chimaera* the postorbital vein passes through a foramen in the posterior corner of the orbit accompanied by the hyomandibular branch of the seventh nerve. In sharks, the vessel merely lies in a post-orbital groove and the hyomandibular nerve, which never enters the orbit, does not share this anterior pathway. It seems likely that the postorbital veins of the two types of fish are homologous and that the different nervous and skeletal arrangements are due to the autostyly and forward compression of the cephalic structures in *Chimaera*. The presence of a foramen rather than a groove, for example, is due to the fusion with the cranium proper of an otic process extending from the jaw joint to the ear region. This cartilage provides the entire lateral wall of the foramen. The forward course of the hyomandibular nerve can be explained by the anterior displacement of the tissues it serves and by the absence of a spiracle and hyomandibular cartilage behind which it would normally pass.

The chimaerid anterior cardinal sinus carries blood over the gill region to the common cardinal in the shark-like manner, receiving in its course the posterior cerebral

vein. The way in which the anterior cardinal and the other large veins of sharks meet to form the common cardinal vessel shows a degree of variation sufficient to preclude the interpretation of the holocephalian arrangement as worthy of special note. Even the connection of the lateral cutaneous vein via the subscapular sinus to this confluence of vessels has its prototype amongst the selachians.

In the postcardiac region the similarity of the selachian and holocephalian plan is still evident. The renal portal and posterior cardinal vessels are substantially the same in both groups. Although the hepatic portal system will receive special consideration below, it may also be generally described as more like that of sharks than that of other fishes. It is in the drainage of the pelvic fins, the ventral body wall, and the liver that significant differences do appear in the chimaerids.

The possession of a subcutaneous system of veins which run unaccompanied by arteries is a final point of likeness which should be mentioned. In sharks as well as chimaerids, the chief vessels in the network, the lateral cutaneous veins, receive segmental tributaries and finally lead to the subscapular sinuses. There are connections elsewhere with deeper vessels in the region of the dorsal and pelvic fins.

That the similarities between the venous systems of holocephalians and selachians do signify an evolutionary relationship is strongly suggested by the fact that their common pattern sets them off distinctly from the bony fishes. Neither ray-finned forms nor lungfishes show the development of spacious sinuses. Allen's (1905) excellent description and beautiful drawings of the circulatory system of the teleost, *Ophiodon*, reveal a complex arrangement of veins of small bore whose homology to vessels in cartilaginous fishes would be difficult to prove. In *Ophiodon*, fine facial vessels empty into a pair of jugular veins directly, since there are no orbital sinuses. The jugular veins, which carry blood posteriorly

over the gill region, are thought by Van Gelderen (1938) not to be homologous to the anterior cardinals in the Chondrichthyes. The posterior cardinal vessels of *Ophiodon*, like those of cartilaginous fishes, receive blood from the renal capillaries, but in other bony fishes there may be direct connections with the caudal vein which never persist in sharks or chimaerids. No actinopterygians that have been investigated have subcutaneous veins except the Thunnidae (and here the veins are accompanied by arteries). As an adjunct to the venous system, teleosts have a well-developed set of lymphatics which all cartilaginous fishes (except possibly *Torpedo*) lack. A glance at the pattern of veins in dipnoans shows an even greater departure from the arrangement found in selachians and holocephalians, since there appear in the lungfishes vessels which are similar to those of amphibians.

Despite the broad similarities between the selachian and holocephalian venous systems there are points of apparent difference whose significance must be considered. A dissection of the hypobranchial region, for instance, does not reveal a pair of easily recognizable, shark-like inferior jugular veins. The area is laterally compressed and occupied by the massively developed hypobranchial muscles whose arrangement leaves no straight channel for these veins to follow. Beneath the muscles, and ventral to the ventral aorta, there exists a mass of loose connective tissue which probably does have fine veins draining blood posteriorly toward the sinus venosus. Allis, who made a preliminary sketch of this area in 1916,² drew a pair of veins here which he interpreted as inferior jugulars. Not finding a hyoid sinus in the usual location, he gave that name to a large vein which begins behind the mandible and

² This and other unpublished sketches of the anatomy of *Chimaera collici* were given by the son of the late E. P. Allis to Dr. A. S. Romer and are in his library in the Museum of Comparative Zoology at Harvard University.

curves dorsally to enter the back corner of the anterior cardinal sinus. It seems more likely, however, that any veins lying deep and near the midline represent auxiliary drainage and that the more lateral, dorsally curving vessel is the inferior jugular vein of *Chimaera*. Although the curious position of this vein suggests that it might be a different vessel from that of sharks, its relation to the base of the gill arches is quite similar and its entry point into the anterior cardinal sinus near the union with the common cardinal is not very different from that shown by Parker (1886) for *Mustelus*. It seems that the inferior jugular vein has been shifted dorsally as the head became laterally compressed, and is not so different after all from that of sharks. It contrasts markedly with the inferior jugular of teleosts which is squeezed medially and in some forms, like *Ophiodon*, exists as a single median ventral vessel for most of its length.

The absence of a hyoid sinus in *Chimaera* may also be due to the relative reduction of the branchial apparatus. In contrast to the large channel which connects the anterior cardinal sinus with the inferior jugular vein in selachians, no major vein appears on either side of the ceratohyal cartilage. Examination with a dissecting scope showed in two specimens a fine vessel which lay anterior to the afferent branchial artery, but the vein was more easily traced along a pathway with the artery out upon the opercular flap than to a connection with the postorbital or anterior cardinal channels. If it is correct to assume that main vessels develop in the embryo as the result of dominance of particular pathways through the initial capillary net, then it is not surprising to find that chimaerids lack a shark-like hyoid sinus. In sharks, where the epihyal cartilage enlarges and develops a close association with the cranium, it is possible that a vein would appear behind it with a connection to the lateral head vein above. In *Chimaera*, where the epihyal never departs

from its serial alignment with other parts of the visceral skeleton, the absence of a special hyoidean vein or sinus might be expected. If one follows this interpretation and accepts this assumption that the non-suspensory hyoid is primitive, it follows logically that the absence of a hyoid sinus may represent an original character rather than a secondary loss. If the holocephalians sprang from an ancestral stock which lacked a suspensory hyoid and a distinctive hyoid vein and then evolved the laterally compressed, short head of the extant animals, neither the space nor the stimulus for the development of a hyoid sinus would have existed.

In pointing out singularities in the precardiac drainage of *Chimaera*, one should not omit mention of the situation of the anterior cardinal sinus. Although it has generally the same location as the sinus in selachians, its route does show one variation: the vein passes lateral to a muscle which Vetter (1878) calls the trapezius internus. In sharks, the sinus lies medial to the entire levator (trapezius) series. Again, this difference could arise from a shift of the musculature rather than the development of a new vein, but it is also possible that there has been emphasis upon an alternate embryonic blood pathway in *Chimaera*. Leaving to one side the possibility of a mistake in the identification of the muscle (the fibers run posteriorly from the subocular shelf to insert upon the anterior edge of the scapula just beyond the last pharyngobranchials), it seems that either a shift in the arrangement of the muscles or the vein must be admitted. How great a significance should be attached to such an alteration remains an open question.

In the postcardiac part of the venous system of *Chimaera* there are differences from the selachian pattern that are more clear-cut if not easier to interpret. The lateral abdominal veins are absent, and the blood which they would have collected is differently distributed. From the pelvic fins and also from a rectal capillary net-

work it is sent directly into the posterior end of the posterior cardinal sinus. A small part of the returning blood may even find its way to the renal portal by a fine connection from the femoral vein. Further forward, the blood from the deep part of the ventral body wall is collected by the ventro-posterior parietal vein which flows posteriorly to a confluence with the renal portal. Finally, the blood from the pectoral fins, instead of joining the flow from a lateral abdominal, enters the common cardinal vein alone. The drainage from the posterior half of the pectoral fin enters what may be more exactly described as a brachial sinus than a brachial vein at the base of the fin and is joined there by the blood from the anterior half of the fin which returns by a vein that passes through a channel in the pectoral girdle. There are two possible explanations for the derivation of this peculiar venous pattern. The first, which cannot be flatly dismissed, is that the ancestral stock of the Holocephali possessed this arrangement of vessels. The second and perhaps more probable suggestion is that the lack of lateral abdominals is secondary in chimaerids as it seems to be in the teleost fishes. The lateral abdominals and their homologues, the ventral abdominal and the umbilical veins, play too large a part in vertebrate development to allow one to dispose of them lightly. Their disappearance might be imagined to have required the longest possible evolutionary course. That these veins have not been described in cyclostomes complicates rather than solves the problem. If their absence represents a secondary loss, one has still no clue to the reason for their absence in holocephalians. If, on the other hand, the lack of lateral abdominals is a primitive vertebrate characteristic, which holocephalians are presumed to have retained, one must then question the homology between the lateral abdominals which selachians have developed and the ventral abdominal vein which appears in the first tetrapods.

The most distinctive feature of the ve-

nous drainage which might merit the same interpretation is the lack of hepatic sinuses opening into the sinus venosus. The anterior portion of the liver, just behind the transverse septum, is very thin, contains no sinuses, and seems to send no blood forward into the heart. The back wall of the sinus venosus, on the other hand, seems entire, but may have vestiges of hepatic openings. Since no injection material can be made to pass through, one might suppose that no passages exist. Slight indentations are visible, however, in a likely location, and a needle can be made to pass, after some probing, without seeming to pierce tissue. If traces of old entrances into the sinus venosus are present, they prove that the lack of hepatic sinuses in the usual location is secondary. Even if it is not certain that such openings are there, it would seem from the design of the hepatic drainage that a secondary arrangement has arisen. The liver is bound to the underside of the posterior cardinal sinus, in its forward portion, and sends to that channel one main vein, two or three other large ones, and several minor auxiliary vessels. In contrast to this pattern, the forward flow from liver to heart is characteristic of every other jawed vertebrate, embryo and adult. In the most deviant pattern, the hepatic sinuses of rays open into the common cardinal veins rather than into the more medial sinus venosus. If the holocephalian pattern were to be judged primitive, it would have to be supposed that it was the sole remaining example of a distinctive circulatory arrangement which existed in ancient times among ancestral vertebrates—a not too likely possibility. As in the case of the absence of the lateral abdominals, it seems more sensible to suggest that the liver drainage represents a great deviation from the usual vertebrate condition and may well have been the product of a long independent evolution.

The search for differences between selachians and holocephalians should be extended to the hepatic portal system, too,

because the homologies between these vessels of sharks and chimaerids are not at once apparent. Upon close scrutiny it seems that the chimaerid veins are more simplified and abbreviated than those of sharks. All of the gastric veins are absent, of course, as are those which drain the spleen and run through mesentery. A short lienopancreatic vein and some small splenics join the vessel returning blood from the posterior regions of the intestine. Consequently, only one vein runs forward to join the intra-intestinal. The union of these two vessels and a smaller one from the anterior intestine and neighboring esophagus creates the hepatic portal. Although it is probable that the lack of mesenteries and the removal of the spleen from its usual place are secondary changes, it is not necessary to assume that the entire pattern of portal tributaries has been only recently evolved. The existence of two sizable branches draining the posterior intestine, an arrangement which has no counterpart in sharks, may not have arisen from any selachian forerunner. It would be tempting to add the lack of gastric veins as another possible preselachian character, because the absence of a stomach has been supposed to be a primitive arrangement; but it cannot be assumed definitely that the lack of a stomach and the minimal development of the spiral valve are primitive rather than degenerate developments. The hepatic portal system, one must conclude, does bear a resemblance to the selachian pattern but may be somewhat secondarily modified. Despite resemblances, on the one hand, and late modifications, on the other, however, it is not impossible that there might be some elements of an older independent pattern still included in the system.

The association of lymphomyeloid tissue with the venous system in the Holocephali is another characteristic which distinguishes these fishes from the shark group. Kolmer (1923), who studied this tissue in *Chimaera monstrosa*, describes it as consisting of a mass of lymphatic cells of varying sizes

mixed with red blood cells in all stages of formation. These cells are supported by a network of fine connective tissue fibers which merge with the adventitia of the wide veins and small arteries that ramify within the mass. If the tissue found in the esophageal wall of sharks and rays is comparable to that which exists in a much expanded state in the chimaerids, one might predicate the presence of this material in the early placoderms. It may have been carried in several lines as a hemopoietic organ, its different location and extent in holocephalians and selachians indicating separate evolutionary pathways. It is harder to imagine that this tissue, which is widespread in sharks and batoids in its esophageal location, should disappear from that place and appear in the head and girdle regions of the Holocephali as they branched off from a shark stem. It is also possible that the tissue of the two groups, although it looks similar under the microscope, may not have a common origin. If that be the case, the hypothesis that chimaerids have been derived from early sharks would have another point against it.

A study of the remaining portions of the circulatory system reinforces the idea that holocephalians and sharks probably arose from placoderm stocks possessing some characters which both groups of fishes have carried to the present day. One has only to dissect the heart in each animal (cf., for example, Lankester, 1878, and Hyman, 1942: 329) to be convinced that chimaerids and sharks, while distinct lines, cannot be widely separated from each other on the evolutionary tree. The hearts of the two types of fishes are identical in their gross anatomy, and markedly distinct from the heart of lungfishes or that of ray-finned forms.³ The only characteristic which distinguishes the chimaerid heart from the shark structure is its relatively small size

³ Lankester (1878), besides describing the heart of *Chimaera*, makes a visibly futile attempt to point out homologies between its arrangement of valves and that in the heart of dipnoans.

(Fig. 4B). Although no measurements were made, it seems that the heart of *Chimaera* would have a smaller capacity than that of a shark of the same size. If one wishes to suppose that sharks and holocephalians have long traveled upon separate evolutionary paths, one must postulate that their type of heart represents the primitive gnathostome structure which has been retained in all cartilaginous fishes and highly modified in bony ones.

The one salient difference in the arterial pattern occurs in the head region. The Holocephali show a type of blood supply to the brain which differs from both selachians and bony fishes in that the pseudobranchial efferent alone reaches the cranial cavity (Allis, 1912). The hyoidean efferent, which feeds the internal carotid in elasmobranchs, forms in holocephalians only a commissure with no continuation running forward to the brain. Even if the investigator assumes that there were in the primitive state two pairs of efferent arteries which sent blood forward to the brain, and that in the Holocephali the more posterior pair has degenerated, he has not disposed of the entire problem posed by the cephalic arteries of the Holocephali. There is also an unusual mandibular artery for which to account. In sharks the lower jaw is supplied by a vessel which leaves the ventral end of the first efferent arterial loop (Hyman, 1942: 324); in holocephalians the mandibular artery runs ventrally from the efferent pseudobranchial, itself a more dorsal branch from the loop. The suggestion has been made by Allis (1912) that the holocephalian vessel, which follows the line of the jaw, represents the ventral portion of the afferent mandibular artery and that the retention of this vessel, which has generally disappeared in other vertebrates, is a primitive feature. If this supposed homology is correct, it would not be possible to derive the chimaerids from a shark group in which the mandibular afferent had already disappeared. However, Marples' (1936) discovery of a similar mandibular

artery in *Squatina*, and his statement of the existence of the same type of vessel in *Polyodon* and certain teleosts, makes questionable Allis' interpretation and any evolutionary theories which might be based upon it.

The only other portion of the arterial system which deviates from the selachian pattern is the efferent branchial series of vessels. In contrast to the distinct loops created in selachians (Hyman, 1942: 324) by the union of well-formed pre- and post-trematic arteries, the poor development of the chimaerid pretrematic branches creates discontinuities in the posterior three collector loops. Allis (1912) believed that he saw four complete loops, but Allen (1905) and Parker (1886) failed to find any. Without doubt, the pretrematic vessels seem secondary to the posttrematic ones. In *Chimaera colliciei*, the ventral ends of the pretrematics diminish in size and the distinct ventral commissures which close the loops were visible only in well-injected specimens. Again, two possible explanations present themselves: either the chimaerid situation represents an early step toward loop-formation or it is the result of a modification associated with the reduction of the gill arch apparatus and its concealment beneath the operculum. There is no way of deciding which theory is more probable.

In conclusion, then, one recognizes that the holocephalian circulatory system resembles that of selachians in numerous ways and yet differs from it distinctly in certain characteristics. In some of its nonselachian features the chimaerid system parallels the structure of bony fish while in others it is apparently unique.

Among the similarities to selachians can be listed the structure of the heart, the general design of the arterial system, the presence in the venous system of great sinuses, and the arrangement of the principal venous sinuses. Pursuing further similarities in the venous system, one must mention the existence of a pair of inferior jugular vessels which are more like the

inferior jugulars of sharks than like those of other fishes, of similar renal portal systems, and of a hepatic portal system that is certainly closer to the type of system found in selachians than to that found in bony fish. Like the selachians, the holocephalians have a system of cutaneous veins and lack lymphatics. As a last point of similarity, even the valves in the chief vessels seem to be located at the same places.

Characters which distinguish the holocephalian circulatory system from that of sharks are found in both the arterial and venous pathways. It is perhaps significant that features of the arterial system which are unique to the Holocephali are all found in the head, a region which is as a whole very highly specialized. Although the incomplete collector loops and the absence of the anterior extension of the internal carotid arteries can be viewed as relatively small modifications of the selachian plan, the significance of the branching of the mandibular artery from the afferent pseudo-branchial is not so easy to interpret.

In the venous system, the absence of lateral abdominal veins represents a great divergence from the selachian pattern and a resemblance to that of ray-finned fishes. With those vessels missing, the brachial veins empty into the common cardinals directly, as is the case in teleosts, and the femoral veins open into the posterior cardinal sinuses. The entrance into these sinuses of blood from the liver is surely a peculiarity developed in the holocephalian line, as such a route is unheard of in any other group of fishes. Whether the absence of a hyoid sinus is also to be interpreted as a secondary development or as a primary arrangement is not clear. The resolution of this question may depend upon the solution of the problem of the status of the hyoid arch with which the hyoid sinus is associated.

In surveying the circulatory system of the Holocephali, one receives the impression that the resemblance to the bony fish, which exists chiefly in the absence of the

lateral abdominal veins, is fortuitous rather than representative of ancestral connections. Since the resemblance to the circulatory system of sharks is more general, the question seems to be whether the holocephalian system is a derivative of the selachian one or whether it has developed in its own path from a system which characterized a placoderm group ancestral to both holocephalians and selachians. An opinion as to which of these alternatives is the more probable could be more strongly supported if the structural arrangements of other systems were brought into evidence. Should they be found to contain characters too primitive to have been derived from the more specialized homologues of sharks, resolution in favor of descent from separate placoderm ancestors would be indicated. If the other systems seem entirely shark-like or differ from the shark pattern in minor ways only, a direct descent from some shark group cannot be ruled out. To extend the comparison between holocephalians and selachians beyond the confines of the circulatory system, then, a review of the nervous, skeletal, muscular, urogenital, and digestive systems is undertaken in the following pages. The study of these systems also provides a check upon the assumption made here that, although similarities between structures of holocephalians and actinopterygians do appear, there is little likelihood of an ancestral affiliation between the two groups.

DISCUSSION OF PHYLOGENETIC CLUES FROM OTHER ORGAN SYSTEMS

The Nervous System

In any study in which the relationships of the Holocephali are reviewed, the nervous system receives primary attention. Its gross anatomy has been studied in detail (Braus, 1898; Cole, 1896; Garman, 1904; Fürbringer, 1897; Nicol, 1950; Wilder, 1877), and microscopic work has been attempted in some areas (Kappers, 1911, 1912; Bäckstrom, 1924; Johnston, 1910;

Nicol, 1950). From the evidence presented in these papers, it seems that the holocephalian nervous system retains some characteristics that must surely be primitive but exhibits peculiarities which are generally interpreted as secondary phenomena.

Although the form of the spinal cord is quite regularly shark-like, the brain is of an extraordinary nature. In its posterior portion it resembles closely the selachian organ, but the telencephalon is unique in the animal kingdom. In *Chimaera* and *Callorhynchus*, this anterior region of the brain extends forward as a long stalk beneath the interorbital septum. It widens finally into a subdivided telencephalic lobe just behind the olfactory bulbs associated with the nostrils. The uniqueness of the arrangement argues for its secondary development. Kappers and Carpentier (1911) have considered the elongation of the telencephalon and feel that it has taken place as a corollary to the enlargement of the eyes. Since the eyes have encroached upon the medial region normally occupied by the cerebral hemispheres, the forepart of the brain has been displaced. Rather than being compressed posteriorly, in the ancestors of the Holocephali, alone among all the animals that have developed enormous eyes, the telencephalon became displaced anteriorly. The result of the forward growth of the telencephalon has been the creation of long brainstalks through which regular connections with the diencephalon are maintained. *Rhinochimaera*, in which the eyes are smaller, the brainstalks not quite so elongated, and the olfactory tracts more selachian-like, may represent an earlier stage in the evolution of this curious arrangement.

Another characteristic of the telencephalon which lends itself to comment of a phylogenetic nature is the development of the pallium. Holmgren, who has studied forebrain morphology in lower vertebrates (1922), has investigated the pallial region in holocephalians, selachians, ganoids, teleosts, and lungfish. He points out that the selachian pallium is inverted to a greater

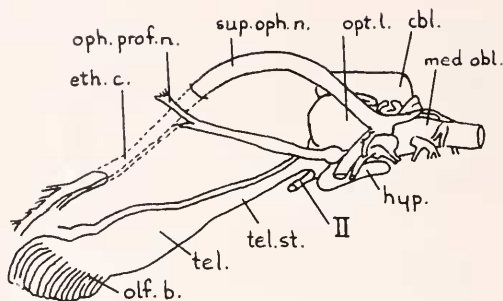


Fig. 1. *Chimaera calliei*. Brain, lateral view. cbl., Cerebellum; eth.c., ethmoid canal; hyp., hypophysis; med.obl., medulla oblongata; olf.b., olfactory bulb; oph.prof.n., ophthalmicus profundus nerve; opt.l., optic lobe; sup.oph.n., superficial ophthalmic nerve; tel., telencephalon; tel.st., telencephalic stalk; II, optic nerve. (After Garman.)

degree than is the case in the other fishes. By inversion he means a rolling medially of both left and right edges of the embryonic neural plates, resulting in their contact dorsally if the two masses of tissue reach the midline as they do in selachians. Evagination of the more lateral portions of the developing forebrain wall gives rise to paired cerebral hemispheres. If nerve cells mass dorsally over the ependymal layer, the dorsal brain wall thickens and the dividing furrow between the hemispheres may be more or less obliterated. The developmental mode which occurs in the Holocephali, however, consists of a lateral rather than a dorsal concentration of nerve cells. The brain roof is then left relatively thin. In extreme manifestations of this latter tendency, the lateral brain walls grow exceedingly thick and may actually evert, leaving the roof to be covered by an expanded tela. This is the case in actinopterygians. A less extreme and perhaps more primitive version of the same condition is found in the lungfish *Ceratodus* (Holmgren and Horst, 1925). The dipnoan has a broad thin roof over the pallium but the moderately thick cerebral walls are not everted.

In holocephalians the laterally thickened pallium is inverted but never becomes continuous over the dorsal midline. There is always a small strip of ependyma bridging

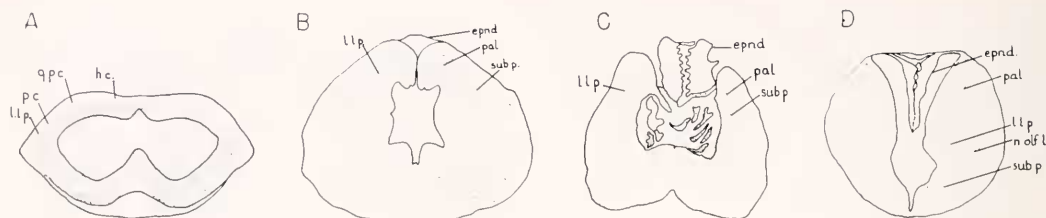


Fig. 2. Transverse section of the forebrain in A, *Acanthias*, B, *Chimaera*, C, *Protopterus*, D, *Lepidosteus*, to show position of the pallium. epnd., Ependyma; g.p.c., general pallial cortex; h.c., hippocampal lobe; l.l.p., lateral limit of pallium; n.olf.l., nucleus olfactorius lateralis; pal., pallium; p.c., pyriform cortex; sub.p., subpallium. (After Holmgren.)

the dorsal gap. The pallium is evaginated to form two separate olfactory lobes which carry separate ventricles forward of the foramen of Munro. The pallium is rather small, being confined to the anterior, enlarged portion of the telencephalon. The brainstalks which connect the anterior enlargement with the remainder of the brain are composed entirely of subpallial tissue.

Kappers, who reviewed holocephalian brain structure in his compendium on the nervous system of vertebrates (1936), grouped the Holocephali with the lower actinopterygian fishes as intermediate between selachians and teleosts. He regarded the inversion of the pallium as carried over from the former and the eversion of the brainstalk walls as presaging the great pallial eversion of the latter. Holmgren disagrees with the conclusion of Kappers, however. He feels that eversion of the subpallial tissue of which the brainstalks consist cannot be regarded as an early stage of the pallial eversion seen in bony fish. In making his interpretation of the phylogenetic position of the Holocephali, Holmgren considers only the true pallium whose limits he has determined by histological study. He reasons that the holocephalian pallium resembles most nearly, in its degree of inversion and evagination, what must have been the type ancestral to that of extant cartilaginous and bony fishes. The development of greater inversion with resulting fusion across the dorsal midline would lead to the selachian condition, whereas the development of thicker and

more widely separated walls would lead to the lungfish-lower actinopterygian-teleost sequence.

Observations upon the microscopic structure of the holocephalian brain have been more fragmentary, and no clear-cut indications of phylogenetic position arise from them. Kappers (1912) has mapped the arrangement of the motor nuclei in *Chimaera monstrosa* and he and several other workers have determined the course of some of the brain tracts in the chimaeroids (Kappers, 1911; Bäckstrom, 1924; Johnston, 1910). One example of the quandary to which these studies have led should suffice. The selachians, with which investigators have sought to compare the holocephalians, are characterized by three telencephalic tract decussations—one dorsal and two ventral. Since the left and right pallial masses of holocephalians do not fuse in the dorsal midline, the dorsal decussation is absent. It is not known whether the fibers which cross dorsally in selachians are channeled through the ventral commissures in holocephalians or whether these fibers are wholly or partially absent. In speaking of the ventral decussation, Bäckstrom goes on to say, "It is, however, possible that a number of fibre connections in this decussatio existing in *Chimaera* are lacking in selachians or vice versa" (Bäckstrom, 1924: 232).

The arrangement of the cranial nerves has also been examined by a worker with the phylogenetic question in mind. Cole, who has dissected these nerves in *Chimaera* in detail (1896; Cole and Dakin, 1906), was

especially interested by the emergence from the brain and the distribution of nerves V, VII, and X. He points out that there is no trigemino-facial complex in *Chimaera* as there is in sharks. Nerve V emerges by two roots anterior to VII and underneath the buccal branch of the latter. It sends sensory and motor fibers to the usual destinations without ever mingling with portions of VII. Contact between these two cranial nerves is limited to a variable degree of binding together of their superficial ophthalmic branches. Nerve VII can be divided into a small motor portion and a larger lateral line component. Cole recognizes that the isolation of the lateral line fibers from the rest of the cranial nerve is also characteristic of other fishes and of amphibians which have a lateral line system and so has no special significance. The tenth cranial nerve of *Chimaera* is distinctive, though, in having its four parts in addition to the lateralis component (three branchial branches and one visceral) completely separate: each arises separately from the brain and each has its own ganglion. Cole dwelt upon the evidence of the primitive position of *Chimaera*, which the separation of the posterior cranial nerves suggests, and concluded: "The discrete nature of the fifth, seventh, and lateral line nerves makes *Chimaera* a very unique fish as regards its cranial nerves, and it is to be presumed that such a simple condition is more primitive than the more complex fusions and interminglings that obtain in other fishes. This separation may, however, be purely secondary, just as the form of the brain of *Chimaera* undoubtedly is, but on the other hand the vagus is also in a very simple and unfused condition in *Chimaera*, and the same may be said of its cranial nerves generally" (Cole and Dakin, 1906: 599).

While Cole was upholding the primitive position of *Chimaera* suggested by the arrangement of its cranial nerves, Fürbringer (1897) was concluding from his comparative study of the occipital nerves of selachians and holocephalians that the latter

were farthest removed from the beginning of the evolutionary line. He had determined that the number of occipital nerves coming through foramina at the back of the skull ranged from five in notidanid sharks to one or none in rays. At first, after finding five such nerves in *Chimaera* and four in *Calorhynchus*, Fürbringer was ready to place these fish on a level with the notidanids. On closer observation, however, he noticed that only the first two resembled the occipital nerves of the selachians in appearance and in their course to the hypobranchial muscles. The remainder looked very much like the succeeding spinal nerves and, like the latter, sent fibers to the brachial plexus. Fürbringer distinguished these nerves as spino-occipital nerves, explaining that in the Holocephali two or three of the anterior vertebrae have been incorporated into the skull bringing their segmental nerves with them. Thus these spino-occipital nerves are not homologous to the posterior occipital nerves of simple selachians but are proof that the holocephalians belong to a "höhere, mehr specialisirte Abtheilung" (Fürbringer, 1897: 446).

The true spinal nerves of holocephalians bear a greater resemblance to those of selachians than to those of bony fishes in that the dorsal and ventral roots retain the large degree of independence which is characteristic of the former group. In *Chimaera*, one can see in each segment of the trunk two roots emerge, give off dorsal rami, and then, as ventral rami, gradually come together. The segmental nerve formed by their union soon divides, and the nerve continues its lateral course as a double-stranded structure. If the two strands represent the reseparation of dorsal and ventral root fibers, the holocephalians would then show a very limited association of dorsal and ventral root elements—an arrangement seemingly closer to the primitive state of complete separation than that shown even by selachians. At the level of the pelvic fin, Davidoff's dissections (1879) show a separation of the strands of the spinal

nerves followed distally by a recombination involving the posterior strand in one segment and the anterior strand from the segment behind. In Davidoff's opinion, this arrangement as well as further connections between the first two nerves which supply the fin suggest the beginnings of a more complex pelvic plexus than is present in other fishes. The holocephalians' lack of a collector nerve in the pelvic region, according to Van der Horst (*in* Bolk, Vol. II, 1934), also sets them apart from selachians, dipnoans, and lower actinopterygians. The plexus at the level of the pectoral fin, however, resembles that of selachians and actinopterygians in being of a cervicobrachial nature. The holocephalians and these fishes are distinguished in this feature from the dipnoans which have, like tetrapods, two separate plexuses in this region. Assessing the various characteristics of the spinal nerves and the plexuses in which they are involved, one might conclude that the holocephalians may show the retention of a relatively primitive arrangement which has been modified to form a unique pattern in the pelvic region.

The last remaining part of the nervous system to be discussed, the autonomic division, has been described thoroughly by Nicol (1950). His study, it must be mentioned, was based only upon *Chimaera collici*. Without attempting to repeat Nicol's description, one may say that he found a very close similarity between the autonomic systems of selachians and holocephalians and substantial contrasts between their type of system and that of bony fishes. For example, he notes that teleosts have well-ordered sympathetic chains connected to the spinal nerves by both gray and white rami. Although the dipnoans show a less well-developed pair of ganglionated chains, the presence of a delicate chain-structure differentiates even these fishes from the selachians and from *Chimaera*. In the cartilaginous forms there is a more or less segmental arrangement of sympathetic ganglia throughout the trunk (and an absence of

ganglia in the tail); but these ganglia are haphazardly connected by a network of nerve fibers and communicate with the spinal nerves by white rami only. Since there are minor differences between the systems of selachians and *Chimaera*, Nicol is of the opinion that the chimaeroids split from the selachian line and have evolved in the final stages on a separate path.

A study of the sense organs produces little evidence which can be brought to bear upon the phylogenetic question. The olfactory, optic, and otic structures in holocephalians are similar to those of sharks, and there are no fossil remains of the first two types of sense receptors from which their hereditary history could be learned. The design of the inner ear in early vertebrates has been revealed through cranial casts, however, making comparisons possible. Stensiö's (1963) cast of the cavities in the cranium of the arthrodire *Kujdanowiaspis* shows a general arrangement of the labyrinth which still characterizes both holocephalian and selachian fishes. Even the endolymphatic duct appears, rising to open upon the dorsal surface of the head. The only point of difference between chimaerids and sharks, of which Stensiö speaks, concerns the structure of the utricle. That of selachians is divided, while the utricle of holocephalians is not. Stensiö thinks that the undivided state is more primitive and that the divided utricle has appeared in certain orders of arthrodires and in elasmobranchs through parallel development. If Stensiö's speculation is correct, the ancestors of holocephalians and early sharks would have been separate but related stocks.

Both Stensiö (1947) and Holmgren (1942a) have included a study of the lateral line system of the Holocephali in their surveys of lateral line systems in fishes and amphibians. Although these authors disagree as to whether a general pattern of head canals can be defined, they state in concert that no explanation of the evolution of the holocephalian pattern is possible at

this time. Holmgren finds it improbable that the holocephalian arrangement could be derived from that of selachians or vice versa. He suspects that the holocephalian system has been reduced from a more elaborate pattern although the absence of embryological studies prevents his speculating upon what the ancestral state might have been. He is forced to abandon the problem with the statement that the holocephalian head canals "could not be identified with lines in any other vertebrate" (Holmgren, 1942a: 21). Stensiö would have liked to have made a comparison between the head canals of holocephalians and those of ptyctodonts, but unfortunately the latter have not been preserved. The anatomy of the sensory canals of holocephalians reveals no more to the investigator than their arrangement. As Garman (1888, 1904) and Reese (1910) have shown, the sensory cells lie in open grooves in *Chimaera*, in slit tubules in *Rhinochimaera*, and in closed tubules in *Callorhynchus*. It is not possible to determine which of these arrangements is primitive or if any one of them is.

Although no single characteristic of the nervous system serves as a key to the evolutionary history of the Holocephali, it is possible to make a reasonable speculation based upon the group of anatomical features discussed above. The survey of the holocephalian nervous system has shown that no portion of it resembles that of any bony fish. Although the anterior extension of the telencephalon, the ramifications of the spinal nerves, and the pattern of the sensory canals are unique, the posterior parts of the brain, the sensory organs, and the autonomic nervous system are strikingly like the shark structures. In drawing conclusions based upon the nature of the nervous system, then, one must lay aside the possibility that the Holocephali might be allied to any line leading to bony fishes (despite Holmgren's view that the dipnoan pallium might be derived from the holocephalian type) and predicate, instead, some degree of relationship to the early

sharks or their ancestors. If one agrees with the assumption that the partially inverted pallium is more primitive than the strongly inverted selachian structure and also with the interpretation of the cranial nerve arrangement as more primitive than that found in sharks, it follows that the Holocephali could not have evolved from early sharks in which the more complex selachian organization was already established. One is left with the hypothesis that the Holocephali have descended from an ancestral group separate from that of selachians but allied to it. This hypothesis allows, firstly, for the retention in holocephalians of the structures assumed to be primitive even though these elements are modified in sharks. Secondly, it provides an explanation for the presence of similar nervous structures in both types of cartilaginous fishes, since these elements may have been characteristic of the larger group to which both ancestral stocks belonged. Thirdly, the hypothesis suggests that the holocephalians developed along a separate line long enough to permit the evolution of the special structures which are unique to them. The alternative theory, that holocephalians are descended from an early shark group, with its corollary that the structures of the nervous system must all be derived by modification of the selachian plan, seems less likely than the above hypothesis which predicates no such close relationship between the two extant groups.

The Skeletal System

Extant holocephalians, like selachians, have a skeleton constructed entirely of cartilage, their only hard parts being isolated placoid scales and the large dorsal fin spine. In the Jurassic forms *Squaloraja* and *Myriacanthus*, however, the dermal elements are more extensive. The fact that there is a greater amount of hard tissue in extinct holocephalians than there is in modern ones gives added support to the idea that the cartilaginous skeleton characteristic of the Chondrichthyes is not the primitive verte-

brate framework but a secondary development. Although this hypothesis does not disallow the possibility that the Holocephali split from the selachian line after the disappearance of bone, it invites one to speculate that the reduction to cartilage may have occurred in the two lines separately.

Comparative studies of the skeleton provide some evidence which can be used in trying to determine where the holocephalian and selachian fishes diverged, but one feels the lack of sufficient fossil data at every turn. Fossils of early sharks are not abundant and among those which have been studied, there is not one whose characteristics suggest that it might have served as an ancestor for the holocephalian line. Moy-Thomas (1936) has offered the cochlodont, *Helodus simplex*, as an ancestral type, but the bradyodonts are themselves distant from selachians. Watson (1938) and Ørvig (1962) have both suggested that the Holocephali have been derived from ptyctodonts, and thus they take the stand that holocephalians have never shared the selachians' evolutionary pathway. A review of the holocephalian skeleton can at best, then, only attempt to define the degree of similarity between it and that of selachians and can try to determine whether a relationship to ptyctodonts or cochlodonts is possible only where comparable structures have been preserved.

A review of the studies of the skull shows that relatively few workers have tackled the head skeleton in its entirety. Only Allis (1917, 1926), DeBeer and Moy-Thomas (1935), and Holmgren (1942b), have looked much beyond the labial cartilages. In making their more inclusive studies, they complain of the lack of data concerning embryonic development: literally nothing exists except the examination of a few embryos by Dean (1906) and Schauinsland (1903). It is a pity that the breeding places of these laboratory-shy fishes are not well-known, for a careful review of a series of embryos from the earliest stages would go

far toward settling some of the questions which Allis, DeBeer, and Holmgren raise.

The first of these questions concerns the developmental interrelationships of the eyes and the cranial cavity. As has been mentioned before, Kappers felt that the depression of the telencephalic space occurred because of the dorsomedial expansion of the eyes. With this conclusion Holmgren would agree. Holmgren surmises from this point that the ancestors of the Holocephali must have been slightly flattened forms with rather dorsally placed eyes. Otherwise, Holmgren reasons, it would not be likely that expansion of the orbits would force the brain downward. It follows, in Holmgren's thinking, that even a more broad-headed cochlodont than *Helodus* would be a likely ancestor for the holocephalians.

In speaking of the structure of the cranial cavity, both Holmgren and Allis take issue with the opinion of DeBeer, Moy-Thomas, and Watson. The latter workers believe that the cranial cavity does not include the passage known as the ethmoid canal, through which the superficial ophthalmic nerves run forward after leaving the orbits. DeBeer and Moy-Thomas (1935) state that this canal is roofed over by a dorsal extension of the orbito-nasal lamina beyond the true cranial roof, and they present a series of drawings of hypothetical evolutionary stages from the uncovered to the covered condition of this supracranial space. In his publication of 1936 in which he presents the case for the descent of the Holocephali from the cochlodont *Helodus simplex*, Moy-Thomas stresses the fact that *Helodus* already shows a dorsally-flared orbito-nasal element.

Allis and Holmgren both hold that since the ethmoid canal is continuous with the cranial space, it is, therefore, a part of it. Allis (1926) suggests that the cranial space anterior to the orbits was cut off indirectly through the pressure of a mysterious embryonic "vesicle" which appears between the midbrain and the forebrain. As the forebrain is pressed downward, the trabeculae

are squeezed outward, eventually rising up and inward to cut the cranial cavity in two. According to Allis' theory, the trabeculae form the floor of the ethmoid canal and the roof of the telencephalic enclosure. The floor under the telencephalon is composed of intertrabecular tissue with perhaps a contribution from the fused palatoquadrate.

Holmgren's interpretation is based more on anatomical examination and less upon flights of fancy. In his study of the heads of fishes (1942b), Holmgren presents photographs of six transverse sections through the orbital region of *Chimaera monstrosa* in which he points out a fine channel, running from the main cranial space forward over the interorbital septum to open into the ethmoid canal. He remarks that in *Rhinochimaera*, which seems to be the most primitive holocephalian, this channel is much wider, making even clearer the continuity of the two spaces. To explain the presence of a floor to the ethmoid canal which divides it from the telencephalic space beneath, he suggests that this cartilage may be a neomorph, citing its very late chondrification as shown by Schauinsland's study (1903) of a *Callorhynchus* embryo. He goes on to hypothesize that, as in some sharks, the superficial ophthalmic nerves of the ancestors of the Holocephali may have run in left and right preorbital canals whose lateral walls were formed by extensions of the supraorbital crest cartilages. Just as these nerves of *Pristiophorus* come inside the cranial space intermittently because of deficiencies in the walls medial to the preorbital canals, so in the Holocephali, through complete disappearance of the cranial walls in this area, the two preorbital canals may have merged with the anterior brain cavity. It is by such a change, according to Holmgren, that the superficial ophthalmic nerves may have come to run within what he considers to be the anterior part of the cranial cavity in the holocephalians. In disavowing the existence of an ethmoid canal as a unique holocephalian character, Holmgren removes one of the structures

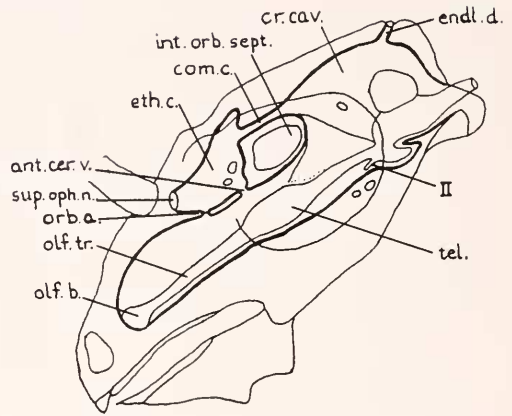


Fig. 3. *Rhinochimaera pacifica*. Neurocranium, lateral view. Cranial cavity with brain outlined. ant.cer.v., Anterior cerebral vein; com.c., communicating channel between cranial cavity and ethmoid canal; cr.cav., cranial cavity; endl.d., endolymphatic duct; eth.c., ethmoid canal; int.orb.sept., interorbital septum; olf.b., olfactory bulb; olf.tr., olfactory tract; orb.a., orbital artery; sup.oph.n., superficial ophthalmic nerve; tel., telencephalon; II, optic nerve. (After Holmgren.)

upon which DeBeer and Moy-Thomas leaned heavily in associating the Holocephali with the cochliodonts.

On the basis of what has been said about the interrelationship between the eyes and the cranial cavity, it becomes plausible to conclude that the chondrocranium probably surrounded a brain space of quite ordinary dimensions in the ancestors of the Holocephali and that the enlarging eyes pressing an interorbital septum between them gradually reduced the median cavity to its present divided condition. If this reasoning is correct, the Holocephali must have long been upon a separate evolutionary pathway, leading from a form like *Rhinochimaera* to one like *Callorhynchus* and finally to the chimaerids. This sequence of evolution is supported by the fact that the interorbital septum in *Chimaera* is even more extensive than that of *Callorhynchus* (Hubrecht, 1877). One would expect the area of the septum to be largest in the group which shows the greatest median expansion of the eyeball.

The otic region of the holocephalian braincase is short, the ear capsule being pressed close against the back of the orbit. Many selachians also show a relatively short otic portion of the skull. If, however, the selachians are descended from primitive forms with an elongate otic and occipital region as Romer believes (Romer, 1964) it becomes less probable that the holocephalian fishes diverged from early selachian stock. The alternative suggestion, that they diverged from the shark line after shortening of the otic region had occurred, places the origin of holocephalians very late, perhaps in the Permian or even in the Triassic period. If Dean (1904) is correct in his identification of *Menaspis*—a Permian form apparently not in the selachian line—as an early chimaerid, it would be better to seek a separate ancestral group for the Holocephali among the Devonian placoderms in which the posterior part of the skull was already short. Ørvig (1962) suggests the ptyctodonts as such a group. In particular, he describes the ptyctodont *Ctenurella* as possessing a short otic region set behind large orbits. Since the ethmoid region of *Ctenurella* slopes downward anterior to the eyes, the general form of the skull does bear a resemblance to that of the holocephalians. The holocephalians are unlike the selachians in having no cartilage wall separating the otic from the cranial cavity. Fossil remains are not sufficiently abundant to indicate whether the presence of a partition was primary, but Stensiö (1963) states that in the arthrodire *Kujdanowiaspis* the two cavities were separated by a thick wall. If the condition in *Kujdanowiaspis* was the general one in arthrodires as it is in modern selachians, one must assume that the confluence of the ear and brain cavities in the Holocephali is a secondary development. Although some teleosts show a confluence, it seems that in each group the modification arose separately.

Another characteristic of the posterior end of the braincase which is very probably secondary is the consolidation with the oc-

cipital region of two or three vertebral elements. Rays and also durophagous fishes (with disproportionate development of the head and shoulder region) show a fusion of skull and vertebral elements similar to that of the Holocephali. Such a modification has surely obscured the ancestral condition in both groups of fishes.

In comparing the braincase with that of sharks, Holmgren mentions particularly the location of foramina. The entryway into the orbit for the superficial ophthalmic nerve is separate from that of the other nerves in both groups, as Moy-Thomas also claims it to be in the coelodont *Helodus*. The foramen for the entrance of the internal carotid artery, however, is farther forward in the Holocephali. The hypophysis grows ventrally into a depression that has an open passage in its floor in the Holocephali, and the notochord, which runs toward it in the base of the cranium, lies in a groove rather than being completely embedded in the cartilage as in sharks. The position of the notochord shows, in fact, not only a difference from that of sharks, but also a similarity to that of certain arthrodires described by Stensiö (1963). In his reconstruction of *Kujdanowiaspis* he shows the notochord lying in a groove on the dorsal surface of the cranial floor as it does in the holocephalians. This similarity to the arthrodires (if it proves to be general) and contrast to the selachians would favor the idea that the Holocephali have direct arthrodiran connections.

The holocephalians also differ from sharks, Recent and fossil, in the possession of a palatoquadrate cartilage which is fused with the chondrocranium rather than being suspended in amphistylic or hyostylic fashion. Since autostyly is known in extant fish only in dipnoans, the palatoquadrate in the Holocephali represents a remarkable departure from the piscine plan. DeBeer, Moy-Thomas, and Holmgren have each devoted attention to the holocephalian palatoquadrate, and, doubtless due to the scarcity of the embryonic material available to them,

their opinions as to its nature are divided. DeBeer and Moy-Thomas (1935) see it as an elongate structure extending posteriorly to the mandibular joint by an otic process which fuses to the cranium against the ear capsule. Holmgren (1942b) recognizes the cartilaginous lamina between jaw-joint and ear region but is not so sure that it is truly a part of the palatoquadrate. It may be, he feels, a separate cartilage in the early embryo. If it is, then the Holocephali are characterized by a very short palatoquadrate element, and only fossil fishes having a short structure should be sought as possible ancestral stock. One might regard both the ptyctodonts and the coeliodont *Helodus* as having a short palatoquadrate if that element terminated at the jaw-joint and the extension to the otic region developed separately, as Holmgren believes it does in holocephalians.

Even though the complete fusion of the palatoquadrate to the chondrocranium seems so distinctive a feature, Holmgren minimizes the distance that this fusion puts between holocephalians and sharks. He points out that in shark embryos the palatoquadrate is connected to the trabeculae by a membrane, parts of which chondrify. One of the chondrifications attaches itself to the palatoquadrate as the orbital process; another fuses to the trabeculae to form the subocular shelf. He asks whether, if the entire membrane should chondrify, firmly uniting the palatoquadrate with the cranium, this process would be so far from what occurs in selachians. A glance at Schauinsland's (1903) illustration of the developing skull of the 65 mm *Callorhynchus* embryo, however, suggests that Holmgren's speculation here may be wide of the mark. At that stage, true cartilage already extends from the palatoquadrate area near the mandibular joint upwards to include the lower half of the orbit. The region in front of this smooth mass of cartilage, as well as that of the problematic extension to the otic capsule, is still in precartilaginous form. It seems that if the holostyly of the

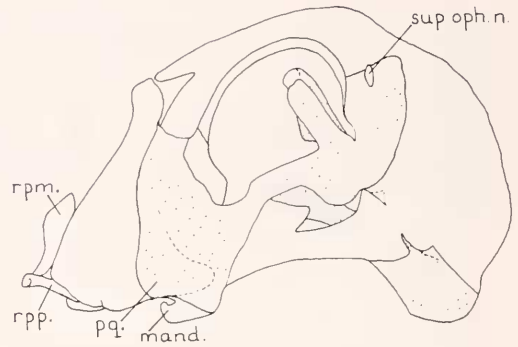


Fig. 4. *Callorhynchus antarcticus*. Skull of 60mm embryo, lateral view. True cartilage, stippled; precartilaginous, white. mand., Mandible; pq., palatoquadrate; rpm., medial rostral process; rpp., paired rostral processes; sup.oph.n., superficial ophthalmic nerve. (After Schauinsland.)

Holocephali was developed through further chondrification of a shark-like arrangement of the palatoquadrate and the trabecula, some indication of the separate nature of these elements should appear in this early stage before the palatoquadrate is developed completely. On the other hand, it is possible that the developmental step for which we are searching has been gradually abbreviated to the point of disappearance. Thus, there are two alternatives: either the separate palatoquadrate never existed even as an embryonic structure in fishes at the holocephalian level, or its development was suppressed later as the line evolved to the present day. Both of these answers imply an evolutionary path long separate from that which led to modern sharks.

It is not inconceivable that holocephalians might have inherited their autostyly from an earlier gnathostome group. That condition was evolved, according to Stensiö (1963) in several groups of arthrodires and apparently was not a rare occurrence. Ørvig admits, however, that in *Ctenurella* (the ptyctodont that he regards as being closely allied to the holocephalian line) the palatoquadrate was not fused to the neurocranium. Moy-Thomas, in advocating a coeliodont ancestor for the Holocephali, points to the autostylic suspension of the palato-

quadrate of *Helodus* as an important similarity between that form and the holocephalians.

A second peculiarity of the visceral arch skeleton in holocephalians concerns the dorsal portions of the hyoid arch. As one might expect from the autostylic suspension of the palatoquadrate, no part of the second arch is enlarged as a hyomandibular. The epihyal and pharyngohyal resemble their serial homologues in the successive branchial arches. The question arises with regard to these elements of the hyoid arch as to whether their state is truly primitive or whether they have been reduced from a specialized, suspensory condition to mimic the simple arrangement of the posterior arches. Holmgren agrees with DeBeer and Moy-Thomas in regarding the non-suspensory condition of the hyoid arch as primitive. DeBeer and Moy-Thomas have examined the holocephalian hyoid arch in detail. In their opinion they have located all its parts, including the pharyngohyal, and judge it to be unmodified. They argue against the possibility that any portion of the hyoid could be fused to the cranium and so lost to view. To make this supposition, one would have to allow the migration of the cartilage dorsal to the lateral head vein, leaving all the other visceral cartilages properly ventral to it. Judging from the unanimity of opinion amongst these anatomists, then, it would appear that a non-suspensory hyoid is one of the primitive characteristics that the holocephalians have carried in their hereditary baggage from early gnathostome times. As an early gnathostome source for the non-suspensory hyoid arch, Watson would have offered the placoderms generally, since he believed them to be aphethochoidean. Stensiö, however, is of the opinion that the early placoderms possessed a suspensory hyoid and that the hyomandibular was reduced to a non-suspensory bar in groups in which autostylism developed. It would not be feasible, according to Stensiö's interpretation, to seek a placoderm ancestor for the

Holocephali if their hyoid arrangement is truly a primary one.

One would expect, in a fish with an elementary hyoid, to find a full gill slit anterior to the hyoid arch like that which Watson predicated for aphethochoidean placoderms. Although a slit does appear in the embryo, it is dorsally placed and soon disappears. The space between the hyoid and the mandible is later crossed by three ligaments: not only is the spiracle absent, then, but the area has been completely rebuilt. It is probable that this change is a modification connected with the forward displacement of the visceral skeleton as a whole and, one might add, of the pectoral girdle behind it. The palatoquadrate is set far forward and fused to the cranium, as we have seen; the hyoid is close behind the mandible and firmly tied to it by the above-mentioned ligaments; and the remaining five arches are crowded up under the posterior end of the cranium. The last two pharyngobranchials and epibranchials are squeezed to a fusion with each other, creating a small flat disc against which the scapula abuts. The entire gill apparatus is reduced and covered by an operculum. This arrangement of the visceral skeleton contrasts sharply with that of extant sharks which have five arches, or in the notidanids and *Chlamydosclachus* more than five, in an extensive pharyngeal region. Fossil forms with a short pharyngeal region (and branchial arches crowded forward beneath the posterior end of the braincase) did exist, and might be a more logical choice as a group ancestral to the Holocephali than the early sharks. The ptyctodonts have been figured by Watson (1938) and by Ørvig (1962) as having only a small branchial area, and Moy-Thomas (1936) describes the coeliodont *Helodus* as having the pectoral apparatus set close behind the head.

The possession of a single median rostral cartilage also distinguishes the Holocephali. In *Chimaera* the rostral cartilage is short; in *Callorhynchus* it is longer and bent ventrally; in *Rhinochimaera* it is longest and

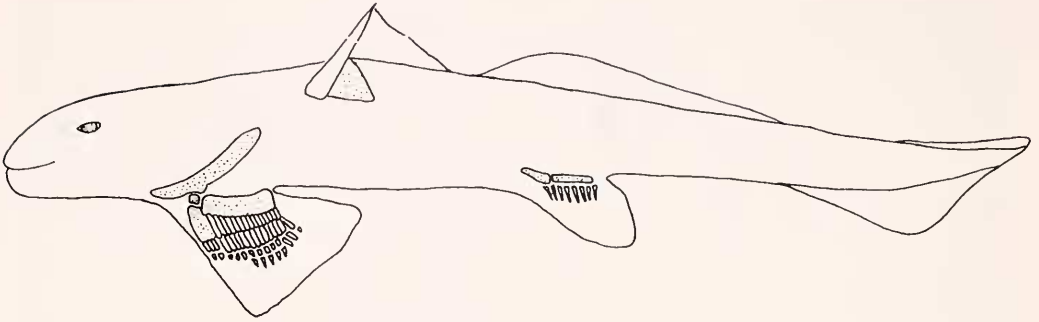


Fig. 5. *Helodus simplex*. Restoration of fish, lateral view. (After Moy-Thomas.)

extends directly forward. Garman (1904) believes that the longest cartilages are the most primitive. This supposition seems reasonable as *Rhinochimaera*, with the longest rostrum, also shows several other characters in what is apparently their earliest form. The fossil holocephalians *Squaloraja* and *Myriacanthus* show well developed rostral cartilages, the former exhibiting some calcification of the element. There, however, the trail ends mysteriously. *Ischyodus*, another extinct form, is figured by Dean (1895) as having a short, blunt head, and the earlier possible ancestors, the coeliodont *Helodus* and the ptyctodont *Rhamphodopsis*, are not known to have possessed rostral structures. *Ctenurella*, according to Ørvig, has a pair of rostral processes but not a medial one. It may be that such structures were not preserved, but in any case the rostral cartilages cannot now be used as Ariadne's thread to reach the light.

Holocephalians, like sharks, have paired labial cartilages. However, in their number and form the labial cartilages differ from the simple, slim bars—an upper and a lower one on each side—which meet at the angle of the jaw in selachians. At the mouth angle in holocephalians, on each side, there are two labial cartilages which meet, but the small superior maxillary element and the larger, flattened inferior maxillary are often fused in the adult. Against the anterior end of the lower jaw there may be a

premandibular labial cartilage (it is absent in *Chimaera collici*); beside the upper jaw there are always a large prelabial and a smaller premaxillary element.

The labial cartilages of the Holocephali were studied for two reasons. Comparative anatomists examined them hopefully as possible clues to the history of the descent of modern chimaeroids, and workers interested in the transition from agnathous to gnathous fish sought in them the remains of the premandibular visceral arches. Despite the descriptions given by Allis (1926), Dean (1906), Garman (1904), Holmgren (1942b), Hubrecht (1877), Luther (1909), and others, the significance of these cartilages has not been surely decided. Their early fossil record is dubious. Ørvig finds some in *Ctenurella* which he thinks resemble those of holocephalians rather than those of sharks. Holmgren suggests that they might be represented in three small elements in *Rhamphodopsis* which Watson (1938) had identified as parts of the hyoid arch. To the suggestion that these elements are modified premandibular arches there are at least two objections: firstly, they are lateral to, rather than medial to, the branchial arteries; and secondly, they show no close resemblance in number or design to visceral arches. Only their position against the upper and lower jaws argues for the assumption. Taking these objections into consideration, Luther (1909: 32) suggests that "Diese Stückchen stellen aller Wahrscheinlichkeit nach einer cäno-

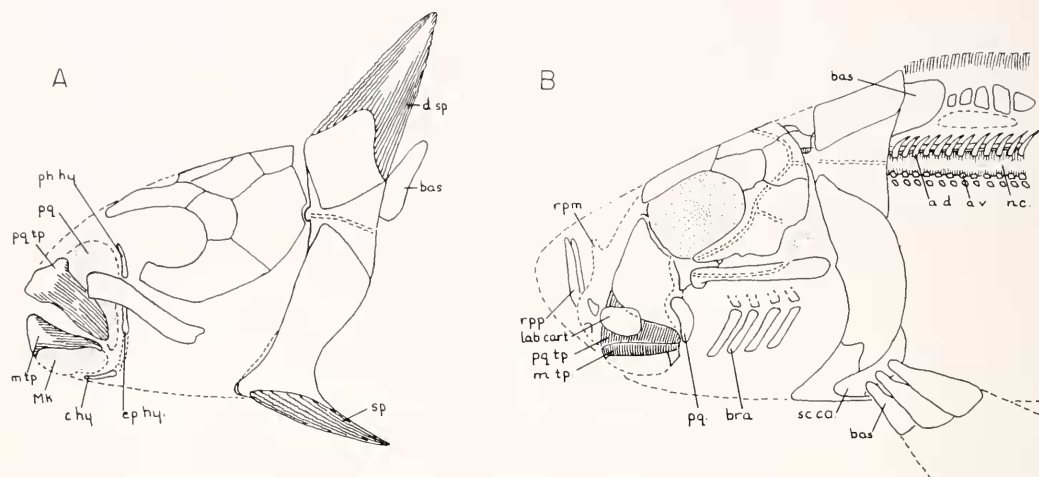


Fig. 6. Reconstruction of the head and shoulder girdle of two ptyctodonts; lateral view. A, *Rhamphodopsis trispinatus* Watson; B, *Ctenurella gladbachensis* Ørvig. a.d., Dorsal arcualia; a.v., ventral arcualia; bas., basal; bra., branchial arch; c.hy., ceratohyal; d.sp., dorsal spine; ep.hy., epihyal; lab.cart., labial cartilage; Mk., Meckel's cartilage; m.tp., mandibular toothplate; n.c., notochord; ph.hy., pharyngohyal; pq., palataquadrate; pq.tp., upper toothplate; rpm., medial rostral process; rpp., paired rostral processes; sc.co., scapulocoracoid ossification; sp., spinale. (A after Watson; B after Ørvig.)

genetischen Erwerb dar, der speciellen mechanischen Bedürfnissen entsprang." All that can really be said with certainty is that the labial cartilages are quite different from those of sharks in their number and form, and in having muscles inserted upon them, and that their present condition implies a long, separate evolution.

The remainder of the axial skeleton is very much simpler to analyze than the skull, but no more directly indicative of the holocephalians' ancestry. The vertebral column presents certain distinctive characteristics which may be listed in a straightforward manner. Anteriorly, it is consolidated radically—not only are the first two or three vertebrae fused with the cranium, but the first seven elements posterior to the occipital articulation are broadly fused with each other to support the strong dorsal spine and an accompanying basal fin-cartilage. True centra are never present; in *Callorhynchus* the notochord is unconstricted; in *Rhinochimaera* and *Chimaera* cartilaginous rings develop within the notochordal sheath. Rabinerson (1925), who studied the comparative anatomy of the vertebrae of carti-

laginous fishes, was of the opinion that the Holocephali were distinct from the selachians in the development of these elements. He recognized that the supra- and hypochordal arch elements of holocephalians bore a greater resemblance to those of selachians than to those of bony fish, but still he held that the similarity was due to convergence rather than to close relationship. Although the holocephalians have retained the primitively unconstricted notochord and in some forms surrounded it with a variable number of skeletal rings, they share with the selachians the tendency to develop arches and intercalary arches above and below it. If Rabinerson is correct in his opinion that the location of the foramina for the spinal nerves differs in holocephalians and in sharks and that the arch units in the two types of cartilaginous fishes have been laid down in a different arrangement, it would seem likely that the holocephalians and selachians evolved separately from a group in which only the general nature of the arch elements was defined.

Among the fossil forms which have been suggested as belonging at the base of the

holocephalian line, only the ptyctodonts seem to show any vertebral structures which bear a special resemblance to holocephalian characters. Ørvig (1962) has stated that *Ctenurella* possessed a fusion of arch elements and an enlarged basal of the dorsal fin. Although Watson (1938) did not find a synarcual in *Rhamphodopsis*, he does figure an element which he believed to be the enlarged basal.

In reviewing the appendicular skeleton of the Holocephali, one is struck first by the fact that its general structure is similar to that of selachians and quite unlike that of bony fish. In both types of cartilaginous fishes the pectoral girdle takes the form of a large and firm U which embraces the body from the ventral side. Articulated with this girdle and with the smaller one in the pelvic region are basipterygia to which are attached jointed fin radials that extend halfway out upon the fin. The remainder of the fin is supported by dermal rays. On closer inspection of the holocephalian skeleton, however, distinctive features do appear. The pectoral girdle is extraordinarily massive and contains a pair of channels within it for the passage of blood vessels. Its scapular process extends extremely far dorsally. Whether the form of this girdle represents a modified selachian type or a different development is not possible to decide. Fossil evidence concerning the deep elements of the skeleton in the shoulder area is meager. Moy-Thomas believed that the pectoral girdle of the coeliodont *Helodus* retained separate left and right halves and if so would not have evinced the consolidation characteristic of the holocephalian structure. Neither Watson nor Ørvig describes the internal pectoral girdle of the ptyctodonts. Since the dermal armor of the shoulder was elaborate, however, one may speculate that inner, non-dermal, skeletal elements were not extensively developed.

The pelvic girdle differs from that of selachians in consisting of separate left and right halves. Although this arrangement

characterizes the bony fishes, too, it may have been a common occurrence in early gnathostomes. Watson describes a pelvic girdle of this type in the ptyctodont *Rhamphodopsis* and Moy-Thomas also attributes such a structure to *Helodus*. The holocephalian girdle also contrasts with that of selachians in developing a strong dorsal process and foramina for the passage of nerves to the fin. One cannot seize upon these differences as demonstrating a significant separation of the holocephalian line, however, as Dean (1909) describes in *Cladoselache*, in the position of the pelvic girdle, a structure with separate left and right portions.

The pterygiophores of holocephalians and selachians, although similar in their general extent, do differ from each other. The basals of the former group are somewhat more compact, there being two rather than three in the pectoral fin and one rather than two in the pelvic fin. The radials in both forms are jointed, although those of holocephalians show a tendency to fuse at their proximal ends. Males of both groups bear pterygiophores modified as claspers. If one accepts *Cladoselache*, with its broad-based fins, long, unjointed radials, and probable lack of claspers, as typical of the ancestors of modern selachians, clearly one must derive the holocephalians from selachians later than *Cladoselache* in which the modern type of fin was already established or predicate a remarkable convergent evolution in the two groups. Again fossil data is too scanty to back either alternative convincingly. Both Watson and Ørvig claim that the ptyctodonts they have examined probably possessed claspers, and, considering the wide variety of clasper-designs among cartilaginous fishes shown by Leigh-Sharpe (1920 ff.), it is not impossible to imagine their having evolved from more than one source. There is no evidence of pterygiophores in ptyctodonts, although Watson speculates that the pelvic fins in *Rhamphodopsis* were probably narrow-based and freely movable.

The conclusion to which this review of the skeletal system leads is twofold. First, although the skull, vertebral column, and appendicular structures of holocephalians have distinctive features, there exists a sufficient similarity between the general plan of the holocephalian skeleton and that of selachians to suggest that the two groups are related in some way. Second, it seems obvious that the holocephalians have very little in common with the bony fishes. There are occasional similarities—the absence of a partition between the otic and cranial cavities and the existence of separate halves of the pelvic girdle—but no really firm basis exists for postulating a relationship between the two lines.

The nature of the relationship between holocephalians and selachians demands analysis. Certainly, the cartilaginous nature of the skeleton in both is a factor to be considered, but the possibility of its having been evolved separately removes the obligation to derive the holocephalians from an already established selachian line. It is not necessary to adhere to the improbable theory that the holocephalian braincase, with its downward-sloping ethmoid and short otic regions, was derived from the early selachian chondrocranium. If the non-suspensory hyoid is truly primitive, a non-selachian origin for it must be sought. If it is a secondary development, the feasibility of its dedifferentiation from the expanded selachian hyomandibular is still questionable. The palatoquadrate is also different in its proportions from the selachian structure if the point of articulation with the mandible marks its posterior limit. Its fusion to the braincase seems to have been an early event rather than a recent modification if its already cryptic embryonic development has any significance. Finally, labial cartilages are structures in the head which it is difficult to visualize as having been derived from their counterparts in selachians. Since the labial cartilages are regarded as vestigial in the latter group, it is not likely that they would have

redeveloped to become the elaborate apparatus of the holocephalians. The median rostral cartilage is harder to assess. The structure is unique and may be a neomorph.

The postcranial skeleton of the Holocephali shows two features which are distinct from their selachian counterparts and difficult to imagine as having been derived from them. The circumchordal elements in chimaerids may be independent developments rather than merely reduced versions of selachian centra. The absence of any type of centra or ring-like structures around the notochord in *Callorhynchus* is possibly a primitive character. The same may be said of the separate halves of the pelvic girdle found in all holocephalians.

The Muscular System

The muscles of the Holocephali have been described by several investigators interested in evolutionary relationships among fishes. Maurer (1912) made a survey of trunk musculature, whereas Edgeworth (1935), Kesteven (1933), Shann (1919), and Vetter (1878) confined their attention to the muscles of the head and shoulder regions. Vetter provided the most exhaustive description of these muscles and assigned names to them. His paper is accompanied by a handsome set of drawings which are helpful in interpreting the text.

In surveying, first, the trunk musculature, one is forced to recognize the similarity of its structure in all fishes. The overriding demands of locomotion as performed by all but a relatively small number of specialized forms have been met by the visibly segmented, more or less zigzagged myotomes which run from the back of the skull and pectoral girdle to the caudal fin. Holocephalians share this general arrangement of the trunk muscles with other fishes but show one specialization which is apparent as soon as the skin is removed: the anterior portion of the ventral hypaxial musculature has become a non-segmented sheet which rises to the level of the lateral line, covering the more dorsal hypaxial bundles. This

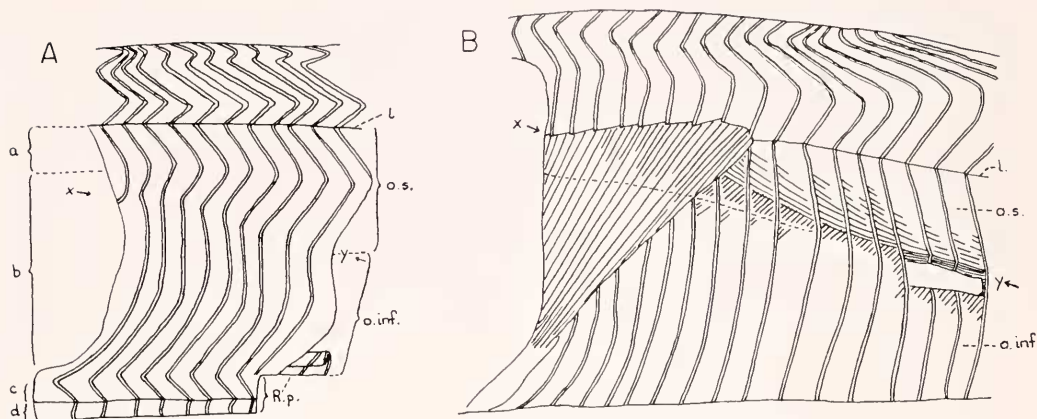


Fig. 7. Trunk musculature: anterior part, lateral view. A, *Chlamydoselachus anguineus*; B, *Chimaera monstrosa*. a,b,c,d, Divisions of hypaxial musculature; l., lateral line; a.inf., inferior oblique; o.s., superior oblique; R.p., rectus profundus; line xy, dorsal limit of inferior oblique. (After Maurer.)

sheet inserts, as one would expect, upon the pectoral girdle. Maurer (1912), who divides the hypaxial muscles into superior oblique, median oblique, and inferior oblique groups, regards the holocephalian sheet as being a modification of the inferior oblique portion. For Maurer, the state of the inferior oblique in the Holocephali represents a more highly evolved condition than exists in any other cartilaginous fish. In the arrangement which Maurer believes is primitive—that seen in *Chlamydoselache* and *Heptanchus*—there is a discontinuity between the inferior oblique and the median oblique (line x-y in his figures) which is set quite far ventrally, leaving much of the median oblique visible. In the course of evolution, the level of the discontinuity rises. The inferior oblique overlaps the median oblique and the latter is gradually reduced. Maurer relates this change to the growing dominance of the pectoral apparatus to which the inferior oblique is attached, and states that the Holocephali represent the extreme expression of this tendency. (He considers sharks but not batoids.) In Maurer's opinion, the Holocephali are also advanced in lacking a ventral rectus muscle of the sort that *Chlamydoselache* shows. That shark

has the two most ventral muscle bundles (c and d in Maurer's figures) rolled medially to form a band bordering the midline. In the sharks, which Maurer regards as more highly developed, and in holocephalians this band does not appear. Throughout his paper, Maurer emphasizes the progression from primitive selachians to Holocephali. It is clear that he regards this progression as having taken place separately from the evolution of the bony fishes.

Shann (1924) noted that fibers of the trunk musculature of fishes are diverted to hold the pectoral girdle in place. Although Shann doubts that it is possible to draw homologies between the various shoulder muscles with absolute accuracy in every case, he does see a basic likeness between the muscles of holocephalians and elasmobranchs. Shann points out, however, that the shoulder muscles of the Holocephali show a far greater differentiation. In sharks, the scapular process is held firm by the antagonistic action of the hypaxial muscles and the cucullaris. The former insert upon the posterior border of the scapular cartilage and the latter upon its anterior edge. In holocephalians, however, both of these groups of muscles are subdivided into external and internal portions. The origin,

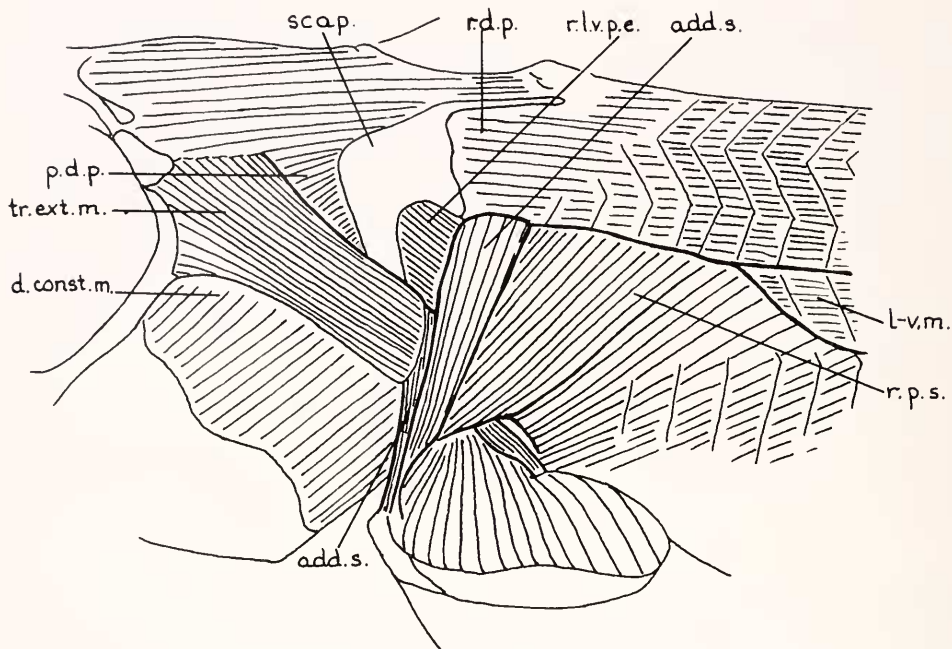


Fig. 8. *Chimaera colliei*. Muscles of the left pectoral region, lateral view. add.s., Adductor superficialis; d.const.m., dorsal constrictor muscle; l-v.m., latero-ventral muscle; p.d.p., protractor dorsalis pectoralis; r.d.p., retractor dorsalis pectoralis; r.l.v.p.e., retractor latero-ventralis pectoralis externus; r.p.s., retractor pectoralis superior; scap., scapula; tr.ext.m., trapezius externus muscle.

insertion, and fiber direction of each differ slightly, clearly a more specialized arrangement. Since the scapular process of holocephalians rises above the level of the horizontal septum, there are also epaxial fibers which insert upon it. In sharks the epaxial muscles are not involved in the shoulder musculature.

In contrast to the more highly differentiated state of the holocephalian shoulder groups, the muscles which are associated with the coracoid region may be simpler than those of sharks. The bases of the coracobranchials are not fused into common coracoarcuals as they are in elasmobranchs. The coracohyoid muscles actually originate on the coracoid cartilage rather than on the fascia over the muscles anterior to it. These aspects of the hypobranchial musculature outweigh, in Shann's mind, the seemingly special, massive development of the cora-

comandibularis, and he emphasizes his impression that the Holocephali are in these structural arrangements more primitive than the sharks and rays.

From the musculature of the paired fins few inferences may be drawn concerning the relationships of the Holocephali. Again, in principle, the fin muscles of all fishes are much alike. To raise, depress, and twist the fins all that has proved necessary are a dorsal and a ventral muscle mass, some fibers of which are drawn into the fin over an oblique course. The holocephalians present but one modification of the general scheme. The proximal portion of the dorsal muscle mass associated with the pectoral fin is differentiated into discrete bands rather than existing as a simple sheet of parallel fibers. The most superficial band originates on fascia at the level of the lateral line and inserts upon the anterior edge

of the fin through a small tendon. From the girdle another band of fibers extends to the front edge of the fin and another to the posterior edge. Between the latter band and the former two, which insert anteriorly, the deeper fibers which cover the fin-radials lie exposed. The distal fibers of the dorsal muscle mass are unmodified and resemble those of sharks. A dissection of the remaining fin muscles in either the pectoral or pelvic region shows that the superficial fibers originate upon fascia or upon parts of the girdle and insert upon connective tissue over the fin basals and radials in the usual way. The deeper fibers originate and insert upon the fin itself as they do in sharks.

The muscles associated with the anterior dorsal fin of holocephalians bear special mention. They consist of a proximal and a distal group of fibers on each side. The proximal muscle mass originates on the plate formed by the anterior vertebral fusion, inserts upon the base of the dorsal fin spine, and acts to elevate the spine. The distal fibers arise from the broad basal cartilage of the fin and insert at the base of the dermal fin rays, allowing the web of the fin to be drawn laterally. This combination of proximal and distal muscles, which is not found in any other cartilaginous fishes, may have been present among the ptictodonts if Ørvig's interpretation of the skeletal elements of *Ctenurella* is correct. In *Ctenurella*, he finds a synarcual element beneath the dorsal fin and a basal piece which could have served as sites of origin for the proximal and distal fibers, respectively.

Much more has been written about the musculature of the head and pharyngeal region than about that of the trunk and fins. From Vetter's (1878) description of the branchial muscles of the Holocephali, one sees that the mandibular arch group resembles the selachian type, lacking the complex subdivision shown by that group in bony fishes. The adductor mass in holocephalians consists of a portion which is

comparable to the quadrato-mandibularis of sharks and, anterior to it, a second part which is regarded as homologous to the selachian preorbitalis. In contrast to the relative size of these muscles in sharks, however, the posterior part of the adductor in holocephalians is smaller than the extensive preorbitalis. The preorbitalis has spread upward over the broad wall of cartilage created in front of the eye, by the fusion of the palatoquadrate cartilage to the neurocranium, and the development of the high cartilage wall in the ethmoid region. The levator and constrictor elements associated with the selachian mandibular arch are not present in holocephalians. The muscles which insert upon the holocephalian labial cartilages, however, appear in no other group of fishes.

The muscles of the hyoid and successive arches contrast sharply with those of sharks. The levator fibers in holocephalians are grouped in external and internal divisions, as was mentioned above, rather than existing as a unified cucullaris. The individual constrictor muscles of the posterior arches, identifiable in sharks, have disappeared. Only the hyoid constrictor remains, and this element is expanded to provide the musculature of the operculum. In the possession of a hyoid constrictor of this kind and in the reduction of the musculature associated with the branchial arches covered by the operculum, holocephalians bear a resemblance to the bony fishes. Kesteven (1942-1943), who accepted this resemblance as evidence of evolutionary relationship, was led into the construction of an evolutionary scheme which is untenable in the face of recent paleontological findings. It might be more correct to suppose that the similarities which do exist between holocephalians and bony fish have come about through convergence.

One could assume, then, that the holocephalian branchial musculature, with its distinctive specializations, developed in correlation with the crowding forward and the

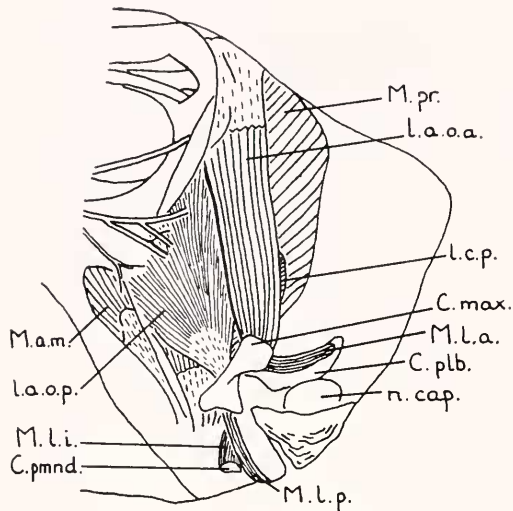


Fig. 9. *Chimaera mantrasa*. Muscles of the head, lateral view. C.max., Maxillary cartilage; C.plb., prelabial cartilage; C.pmnd., premandibular cartilage; l.a.o.a., levator anguli aris anterior; l.a.o.p., levator anguli aris posterior; l.c.p., levator of prelabial cartilage; M.a.m., adductor mandibulae; M.l.a., labialis anterior muscle; M.l.i., labialis inferior muscle; M.l.p., labialis posterior muscle; M.pr., preorbitalis muscle; n.cap., nasal capsule. (Adapted from Luther.)

fusions which took place within the visceral and cranial skeleton during the independent evolution of the Holocephali. As the gill arches became compressed under the occipital region and the extrabranchial cartilages spread to form an opercular cover, the branchial constrictor muscles gave way in favor of an expanded hyoid constrictor sheet. The branchial levators, adductors, and interbranchials all became reduced in accordance with the reduction and compression of the cartilages of the arches. Since the mandible is short in holocephalians and forms only a shallow curve, the ventral portion of the hyoid constrictor (which reaches the midline in sharks as the interhyoideus) apparently shifted the origin of its most anterior fibers forward to the connective tissue on the posterior ventral edge of the mandible. There being no division between the palatoquadrate and the ethmoid region of the cranium, the

muscles innervated by the trigeminal nerve spread over the entire anterior region of the head. The divisions of this muscle which insert upon the labial cartilages would seem to be late developments. If the branchial muscles of the Holocephali evolved as suggested here, it would be logical to seek an ancestral stock in which the shortening of the head region had already begun. The ptyctodonts show such a condition and may thus be a better choice as ancestral material for the holocephalians than the longer-headed coelodont *Helodus* or any early selachian.

In sum, then, one recognizes in the muscular system of the Holocephali a number of similarities to the system of sharks, many characteristics which are certainly specializations peculiar to the group, and certain features which are comparable to those of bony fishes. Among the holocephalian muscles, which show some resemblance to selachian counterparts, are the trunk and fin muscles, the hypobranchial muscles, and the adductor muscles of the mandibular arch group. Within each of these groups of muscles, however, some unique arrangement appears: the sheet-like, nonsegmented inferior oblique among the axial muscles; the special nature of the proximal pectoral extensors among the fin muscles; the great expansion of the pre-orbitalis in the mandibular arch group. Besides these peculiarities, the complexity of the shoulder musculature, the anterior dorsal fin muscles, and the muscles which insert upon the labial cartilages must be regarded as singular and non-selachian in nature. The sole resemblance of the holocephalians to the bony fish lies in the presence of an expanded hyoid constrictor and reduced musculature of the posterior branchial arches. In assessing this similarity as evidence of convergence rather than relationship, one may well be on solid ground. Estimating the significance of the similarities between holocephalians and selachians is more difficult, however. Since the musculature of the holocephalians shows no

characteristics which are clearly more primitive than those of any shark—unless the absence of the common coracoarcuals be so considered—the possibility of its evolution from a generalized selachian pattern cannot be ruled out. On the other hand, the axial and branchial musculature shows many specializations which are closely allied to the design of the skeleton. If one considers the evolution of the muscular system in correlation with that of the skeleton, it seems more logical to suppose that it developed, as the skeleton seems to have done, from a more ancient root than the early selachian fishes. And if one leans toward the idea of descent from a ptyctodont rather than from a selachian group, it may be perhaps because it is easier to imagine building holocephalian musculature upon a ptyctodont frame, especially in the head region, than it is to derive it from shark-like origins.

The Urogenital System

Little research has been done on the urogenital system of the Holocephali. Studies of its development are lacking and the histology of its component organs has received only cursory attention (Burlend, 1910; Leydig, 1851). Its gross anatomy, which is known, is almost exactly like that of sharks and quite different from that of bony fishes.

A glance at the reproductive organs of the female holocephalian reveals an arrangement which is exactly like that of many selachians. Both ovaries, equally well developed, are set far forward in the body cavity. The oviducts run lateral to the ovaries to open with a common ostium in the extreme anterior end of the coelomic space. The shark-like nature of this arrangement is emphasized if one reviews the female genital system of other types of fishes: in almost all teleosts the oviduct is continuous with the ovary so that the eggs, which are produced in large numbers, are at no time free in the coelom. In a few forms like the trout, the ovary does

release eggs into the body cavity, but the ostium of the oviduct may be located more posteriorly than it is in the cartilaginous fishes and the oviduct itself never shows the specialized areas characteristic of the oviducts in Chondrichthyes. In species which are descended from the earlier parts of the bony fish line (*Polypterus*, *Acipenser*, *Amia*, *Lepisosteus*), the ovary is unenclosed but is either more elongated or located more posteriorly. The oviduct in these forms differs in design from that in cartilaginous fishes. Admittedly, the position of the gonads and ducts in the female lungfish corresponds more nearly to that of the Holocephali. The lungfish ovary is much longer, however, and the oviducts are unspecialized and have separate ostia.

The specialized regions of the holocephalian oviduct resemble closely the selachian type. Prasad, who made a series of histological studies of such specialized areas, said, "... the nidamental glands of *Hydrolagus collicii* exhibit a structure very similar to that of a typical oviparous elasmobranch..." (Prasad, 1948: 57). One could say, in view of the similar reproductive habits of oviparous elasmobranchs and holocephalians, that their similarly specialized oviducts were a parallel development, but there is no evidence to disprove the idea that these fishes may have inherited both the habits and the structures from an earlier—even a very much earlier—common stock.

In searching for differences between sharks and holocephalians, one might seize upon the fact that adult female sharks have a cloaca whereas their holocephalian counterparts do not. However, the importance of this point diminishes when one sees that the young female holocephalian has at least a deep urogenital sinus which disappears as the uteri enlarge and press outward in the maturing animal. The one unique structure possessed by the female holocephalian is the so-called seminal vesicle. Hyrtl, who reported in 1850 on the indented blind sac which opens just posterior to the anus,

thought that it functioned as a "Samen-tasche," but Burlend (1910) showed that it was glandular. Redeker (1898) saw in this sac a possible homologue of the digitiform gland of sharks: if the rectum of the holocephalian were pulled inward from the surface, drawing the "seminal receptacle" in with it, the latter structure would be in the same relation to the hindgut as the gland of the shark. It is probable that, whatever its mode of formation, the blind sac, which is not found in any other vertebrate, represents a minor specialization which has occurred in the later evolution of the Holocephali.

The reproductive system of the male holocephalian is as shark-like as that of the female. In both types of fishes the testis is connected by vasa efferentia to a highly coiled epididymis through which sperm are conducted to the more posterior and wider portion of the vas deferens. The vasa efferentia of the shark represent transformed anterior kidney tubules which lead into the embryonic Wolffian duct, and it is presumed that the efferent ductules of the Holocephali are homologous structures. The anterior part of the kidney in immature sharks and chimaerids has glomeruli in it, but these disappear during growth toward sexual maturity. The anterior part of the kidney transforms itself from an excretory to a secretory organ and is then known as Leydig's gland. In holocephalians, as in sharks, its secretion, which passes through short ducts to the epididymis and vas deferens, serves as a fluid matrix for the suspension of the sperm. The posterior portion of the kidney in both kinds of fishes remains excretory, sending urine through one or more ureters which empty into a urogenital sinus. In commenting upon the arrangement of pathways in the male system, Van Oordt says, "hinsichtlich, der Abführung der Spermien stimmen die Holocephalen mit den Selachiern überein" (Van Oordt, in Bolk, 1938, Vol. V: 750). In resembling the selachian system so closely, the male reproductive system of the holocephalians

is markedly different from that of the bony fishes. In the latter group one finds either a duct for sperm which is separate from the original archinephric duct or the tendency to develop such an arrangement. Even in *Acipenser*, where the expression of this tendency is minimal, the urogenital system is distinguished from the selachian and holocephalian types by lacking a secretory portion derived from the anterior end of the kidney. No bony fish develops an accessory organ comparable to Leydig's gland.

Given the great degree of similarity between male selachians and holocephalians, investigators have tried to define the relatively small points of difference which do exist. It has been observed, for instance, that the number of vasa efferentia varies. In contrast to one in *Scyllium*, *Chimaera monstrosa* has five or six. Borcea (1906: 349), who made an extensive study of the urogenital system of elasmobranchs, considers that "le nombre des vaisseaux éférents est plus élevé et le canal longitudinal de l'épididyme est plus long chez les types les plus primitifs." In making this statement, Borcea had in mind the fact that the batoids are characterized by a few or only one vas efferens.

Another minor difference concerns the posterior region of the vas deferens which is enlarged to form an ampulla (Van den Broek's term) or a sperm vesicle (Burlend's term). In both sharks and chimaerids, the inner wall of this structure is thrown into folds which divide the lumen of the duct. In sharks like *Scyllium*, however, the partitions are as simple as septa in a mushroom cap, whereas the inner walls in a large section of the chimaerid ampulla run into one another in a more complex fashion, cutting up the space within the passage into interconnecting compartments. One feels, upon studying these septa, that their different design is less important than the fact of their presence in both holocephalians and selachians. The appearance of these structures is a remarkable point of similarity in two forms whose lines (in consideration of

other organ systems) seem to have separated far back in time.

This same idea may be emphasized in the matter of the claspers of the male. Before describing the differences which exist between these structures in sharks and holocephalians, one must dwell a moment upon the fact that claspers, which are not a common vertebrate characteristic, do appear in a generally similar form in both of these groups of fishes. It would seem, at first, that the possession of such claspers is signal proof of the close relationship of sharks and holocephalians. The major obstacle to the acceptance of this idea lies in the fact that *Cladoselache*, a form apparently antecedent to modern sharks, shows no claspers. If it really had none, then the holocephalians must have developed their claspers independently. That they did so is not an impossible assumption. It appears that claspers may not be as peculiarly elasmobranchian a character as one would assume from a study of extant fishes. If Watson (1938) and Ørvig (1962) are correct in postulating the presence of claspers in *Rhamphodopsis* and *Ctenurella*, respectively, it may be that these structures were possessed by a number of placoderm groups. If that was the case, holocephalians and selachians might bear claspers inherited from separate ancestral stocks. In support of this hypothesis one might cite Ørvig's finding of a pair of dermal spines anterior to the pelvic girdle of *Ctenurella*. He believes that these spines may have been associated with anterior claspers, adjuncts to the reproductive system found in holocephalians but not in elasmobranchs.

The elaborate array of claspers characteristic of holocephalians sets these fishes apart from other cartilaginous forms. No other type of fish has either the aforementioned anterior claspers in front of the pelvic fins or the strange median frontal clasper or tenaculum set upon the dorsal surface of the head. In all extant holocephalians the anterior claspers are represented as small, gripping structures which are concealed in

a pouch when not in use. Leigh-Sharpe (1922) believes that the prepubic processes found in *Squaloraja* supported anterior claspers in that Jurassic form. There are no reports of these structures in earlier fossils, however, except for Ørvig's mention of the spines in *Ctenurella*. Since Ørvig found no trace of a tenaculum in *Ctenurella*, the earliest form of that structure is known from *Squaloraja* and its contemporary, *Myriacanthus*. The tenaculum in those fishes was a long pointed protuberance. In living holocephalians, the tenaculum is smaller and rounded at its distal end.

In a lengthy series of papers Leigh-Sharpe (1920 ff.) presents a review of elasmobranch and holocephalian claspers. He describes the claspers of *Chimaera* and *Callorhynchus* as having two branches and suggests that these branches represent the ultimate and penultimate pelvic fin radials. He believes that claspers of this type are primitive. However, *Rhinochimaera*, which is thought to be the most primitive holocephalian in terms of its other systems, has an unbranched clasper more nearly like that of sharks. Leigh-Sharpe (1922) includes a drawing of a clearly preserved clasper of the fossil *Squaloraja* which shows a single but unusually broad structure terminated by a group of small, dermal hooks. Since the clasper of *Squaloraja* is unique in form, and since *Squaloraja* lived in Jurassic times when the holocephalian line was already established, one cannot be sure that the claspers of this fish give evidence of the original nature of the holocephalian structures.

In his classification of the cartilaginous fishes according to the type of clasper they show, Leigh-Sharpe sets the Holocephali amongst the primitive forms for still another reason. They have not developed the abdominal structures—a pair of muscular cavities called siphons—which play a role in sperm passage during the copulation of most elasmobranchs. Holocephalians do have a different sort of cavity, though, located in the proximal portion of the clasper.

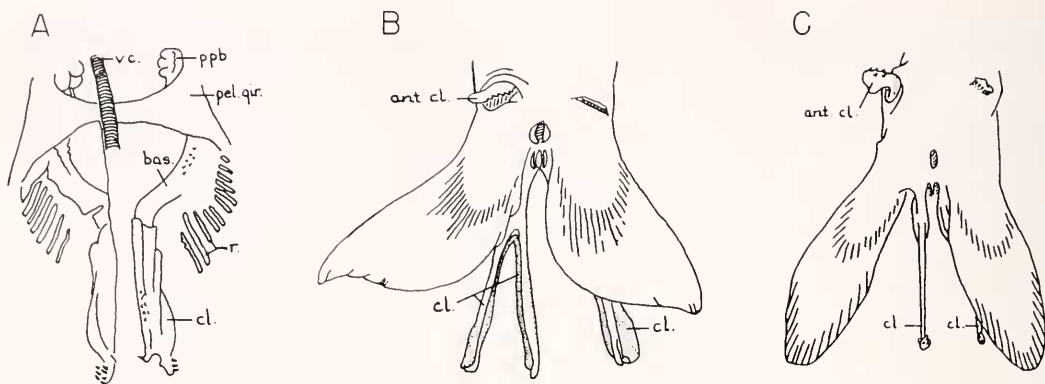


Fig. 10. Claspers of various holocephalian forms. A, *Squalaraja*; B, *Chimaera manstrasa*; C, *Rhinachimaera atlantica*. ant. cl., Anterior clasper; bas., basal; cl., clasper; pel.gir., pelvic girdle; ppb., prepubic processes; r., fin-rays; v.c., vertebral column. (After Leigh-Sharpe.)

Leigh-Sharpe interprets this cavity as homologous to that of *Chlamydoselache* and so brackets these fishes together. Surely a common category for these forms stands on shaky ground. The Holocephali should probably be set apart even here if the presence of their curious frontal and anterior claspers is taken into consideration.

Although the kidneys have not been thoroughly examined histologically, their gross anatomy and their relationship to the genital organs have been well described (Burlend, 1910; Leydig, 1851). There is no doubt that these organs, too, are like those of elasmobranchs and quite different from those of other fishes. Unlike the kidneys of the cartilaginous forms, those of bony fishes never become closely involved with reproductive structures in the male and, in both sexes, are generally uniform in tubule-structure throughout their length, undergoing neither transformation nor degeneration at the anterior end as the animal reaches maturity. It is not necessary to lean entirely upon structural resemblances to predicate a possible relationship between the Holocephali and the Selachii either. The excretory systems of both groups bear the same distinctive functional earmark: the kidneys resorb urea selectively and

maintain that substance in the bloodstream in unusually high concentration.

In adult holocephalians, as in sharks, urine is produced in the posterior regions of the kidney and drained by specially developed ureters. This arrangement contrasts with that of bony fish in which urine is produced throughout the entire kidney and is removed through the opisthonephric duct. In cartilaginous fish of the male sex the anterior kidney and the Wolffian duct become part of the reproductive system as was mentioned before. In females, despite there being no secondary use for the anterior region of the kidney, that portion degenerates and the Wolffian duct stretches forward and ends blindly. In the animals of both sexes the kidney gives some hint of its originally segmented nature. Especially in the anterior region traces of segmental divisions remain. The segmental blocks are particularly noticeable in the male, because ducts leave the gland of Leydig at segmental intervals.

Borcea (1906), in the study to which reference has already been made, is plainly of the opinion that the elasmobranchs represent the primitive vertebrates from which all the others have descended. Although most students of evolution no longer agree with that premise, they still admit the pos-

sibility that certain characteristics of cartilaginous fish may have been carried over from their primitive ancestors at the placoderm level. With this idea in mind and in consideration of the similarity of the urogenital systems in holocephalians and elasmobranchs, one may find interesting the following comment of Borcea: "C'est le groupe des Elasmobranches, qui nous montre la succession de ces trois stades (of the evolution of the vertebrate kidney) avec la plus grande netteté. D'une part, ils présentent l'état néphridioïde . . . plus nettement que n'importe quel autre groupe de Vertébrés. D'autre part, ils sont parmi ceux-ci, les animaux les plus primitifs chez lesquels les glandes génitales entrent en relation avec le rein et son uretère primaire et alors la série des changements se montre d'une façon très manifeste. Chez les Elasmobranches la division de l'uretère primaire est tout à fait nette. Chez les plus primitifs d'entre eux ce n'est qu'à l'état adulte (en relation avec la maturité sexuelle), qu'on constate la modification du rein supérieur" (Borcea, 1906: 251).

Disregarding Borcea's use of the term "état néphridioïde" which summons up an argument quite apart from the subject of this paper, one can still see in his statement reasons to support the thesis that the elasmobranch urogenital system is primitive rather than secondarily simplified. If the system is primitive, then there is an alternative to the theory that the holocephalians, whose urogenital organs seem shark-like, must therefore have diverged from the elasmobranchs relatively late. It is possible to speculate that, as evidence drawn from other structures suggests, the holocephalian and elasmobranch lines did split far back among their placoderm forebears, and that both groups of fish have carried to modern times the type of urogenital system which those early vertebrates possessed. That a system of this type may have become widespread in primitive gnathostomes generally is suggested by the development in all vertebrates except the bony fishes of an inter-

relationship between the testis and the kidney similar in principle to that which appears in the cartilaginous fishes. This idea is supported further by the emphasis, again in all vertebrates except bony fishes, upon the posterior portion of the kidney as the part chiefly responsible for excretory function.

To summarize the foregoing points, one may state that the urogenital system of the holocephalians resembles the selachian system closely. In the position of the gonads, the specialization of the accessory ducts, the nature of the kidney, the development of accessory ureters, and the possession of claspers on the pelvic fins of male animals, the two groups of cartilaginous fishes are remarkably alike. The type of urogenital system they share is distinct in all of these features from that of bony fishes. The kidneys of holocephalians and selachians are set apart from those of all other vertebrates by their ability to resorb urea selectively and return it to the circulating blood. The major point of difference between holocephalians and selachians lies in the possession by the former of claspers anterior to the pelvic fins and of a median tenaculum.

Although the remarkable similarity of the urogenital system of holocephalians to that of selachians could be cited as evidence of the evolution of the Holocephali from the selachian line, there appears to be an alternative to that hypothesis. Since it seems possible that the urogenital system of cartilaginous fishes is truly primitive and if so may have existed in a number of early gnathostome groups, holocephalians and selachians could have evolved from two separate ancestral stocks. Both types of cartilaginous fishes could have retained the urogenital system in its ancient form. This theory presumes that the holocephalian and selachian claspers were not derived from the same source. The possibility that ptyctodonts possessed claspers allows one to believe that there may have been more than one source of those structures at the placo-

derm level. The presence of anterior and frontal claspers in living and fossil holocephalians but not in selachians increases the probability of the existence of a separate placoderm ancestor for the holocephalians.

The Digestive System

The search of the digestive system for evidence of hereditary relationships turns up a profitable thread or two and also reveals several alleys which end blindly. As might be imagined, an investigation of the structure of the teeth gives rise to speculations based on firmer ground than does an examination of the digestive tract itself or its associated glands.

Holocephalians have three pairs of toothplates. The smallest, called vomerine plates, are located in the anterior portion of the upper jaw immediately in front of the larger palatine pair. The mandibular plates of the lower jaw are the largest, being equal in length to the other two combined. A comparison of the sections of these teeth figured by Brettnacher (1939) with those of cochliodonts shown by Nielsen (1932) suggests that the two tooth-types are not similar, as Moy-Thomas (1936) had maintained. A difference if it does exist, is important, because the structure of the toothplates was one of the main supports of the theory that the Holocephali are descended from bradyodonts. If the teeth of the two groups are truly unlike, and if the presence of holostylic jaw suspension in both groups is not as important a factor as Moy-Thomas thought it was, then the case for close relationship becomes very much weaker.

The discrepancies in tooth-type become apparent when descriptions of the internal structure of the teeth of each are set side by side. Eigil Nielsen (1952: 34) gives the now classic description of the bradyodont type: "This Bradyodont structural type is especially characterised by possessing a system of numerous, more or less parallel vascular canals ascending through the greater part of the crown, but ending

blindly just below the tritoral surface. The ascending canals are lined with layers of dentine, and the dentine around each canal is separated from that around the other canals by a hard tissue, described as enamel by me in 1932."

The chimaerid toothplate has been examined, described, and figured by Bargmann (1933) and Brettnacher (1939). Their accounts of the histology of the toothplates agree, although the terminology that they use in their descriptions is not exactly the same. The outer surface of the crown of each plate as well as its embedded portion consists of a type of dentine which Brettnacher calls "Hüllendentin" and Bargmann calls "Manteldentin." In areas where epithelium comes in contact with the toothplate, there is a superficial layer of very hard material which, for Brettnacher, is true enamel, and for Bargmann merely a specially transformed part of the "Manteldentin." In the interior of the tooth, according to both men, there is a *meshwork* of dentin trabeculae rather than parallel dentinal tubules. Brettnacher gives these trabeculae the special name of "Balkendentin" (because they form supporting beams), although he does state that they are formed by an extension of the odontoblast layer which creates the "Hüllendentin." Bargmann uses the term "Manteldentin" to embrace the trabeculae as well as the peripheral layer. The spaces in the trabecular region are pulp channels which Bargmann says are slowly obliterated in the pressure-receiving parts of the plate by deposition of circumpulpar dentin.

Jacobshagen, who relies upon Brettnacher's work, has included the chimaerid toothplate in his review of the structure of selachian teeth (1941). As he presents his figures and comparative descriptions, one sees that there could be logic in his reasoning that the internal arrangement of the holocephalian plate is a primitive variant of the dentinal pattern still in existence in extant elasmobranchs. Both holocephalians and selachians show the outer "Hüllenden-

tin" covering an inner trabecular meshwork. The categories that Jacobshagen establishes depend upon the thickness of the outer dentin layer and the amount and distribution of the inner "Balkendentin."

Jacobshagen does make a separate category for the toothplates of the Holocephali, not only because of their plate-like structure, but also because they contain a unique material which both Brettnacher and Bargmann describe. Brettnacher calls it "primary dentin" and Bargmann uses the old term "Kosmin" to refer to it. This substance is found within the pulp channels in several regions within each plate. Sometimes the Kosmin appears in pearl-like masses strung in rows; in some teeth the "pearls" seem coalesced to form an elongated bar. All the investigators who have discussed Kosmin regard it as an ancient vestige. Schauinsland thought it represented the remains of fused cylindrical teeth. Bargmann discards this idea, however, for the teeth of younger specimens show Kosmin in its undivided bar-like form. The rather periodic, pearl-like division, he feels, is a later manifestation. Bargmann has his own theory: he compares the structure of Kosmin to the structure of the surface knobs on *Cephalaspis* plates, and speculates that in the evolution of the Holocephali this early type of hard tissue may have sunk inward.

Brettnacher and Jacobshagen point out that dentin in general may have evolved from a relatively soft substance, penetrated by widely spaced, branching tubules to a much harder material with close-ranked parallel tubules. With this idea in mind they both consider that the dentin-tissue in the Holocephali is of the primitive type, the toothplate deriving its strength from the arrangement of the dentinal trabeculae rather than from the hardness of the dentin itself.

As these workers describe and discuss the structure of holocephalian toothplates, it seems less and less likely that these plates have much in common with cochlodont teeth. The latter consist of what Ørvig

(1951) would classify as "tubular dentin" and in Nielsen's figures look singularly different from anything produced by the Holocephali. The "Balkendentin" which fills the chimaerid toothplate seems more akin to Ørvig's osteodentine in its arrangement and its apparent mode of development.

If it is not correct to associate holocephalian and cochlodont teeth with each other, one is free to seek other relationships. It seems not unreasonable to connect the chimaerid structure with that of ptyctodonts. Ptyctodont plates have been studied histologically most recently by Gross (1957) and Ørvig (1957). Gross found very little difference between the teeth of *Rhynchodus* and *Ptyctodus*, and his general description reveals a surface layer of dentin supported from within by dentinal trabeculae which formed a network. Against these internal trabeculae in tritoral areas, what Gross calls a secondary dentin was laid down. It would have been interesting if Gross had referred to the work of Brettnacher and Bargmann. Without such a reference one cannot be sure whether Gross considered the dentin material which he mentions equivalent or similar to that of the Holocephali. It is impossible from Gross' description, for instance, to tell whether he saw something like Kosmin. It appears that he did not.

Ørvig's description of *Paleomyilus* is more puzzling. He states that the *Paleomyilus* toothplate is much like those of *Ptyctodus* and *Rhynchodus*, and in the number of its tritoral columns even more like the Mesozoic and Cenozoic Holocephali. But he describes these tritoral columns as being separated by acellular bone, while in holocephalians they are separated by an interstitial substance "not unlike enamel." He refers to the chimaeroid columns as being of a peculiar tubular dentin "*sui generis*." Since describing the *Paleomyilus* toothplate in 1957, however, Ørvig has revised his terminology. For hard tissues which grow inward toward the basal region of the toothplate, including tritoral columns, he has introduced the name "pleromic hard tissue." Although he does

not mention *Paleomylus* specifically, in a forthcoming book he indicates similarities between the pleromic hard tissue of ptyctodont arthrodires and holocephalians. He emphasizes the difference in arrangement of the pleromic tissues of ptyctodonts and holocephalians, on the one hand, and of bradyodonts, on the other, by classifying the pleromic material of the former as columnar and of the latter as coronal.

Although it is usual to analyze the histological structure of teeth in an effort to derive evidence of phylogenetic significance, it might be well to keep in mind the possibility that convergent evolution could have brought about similar structure where no relationship exists. Radinsky (1961), who has found similar patterns in the dentin of bradyodonts, batoids, selachians, and dipnoans, is of the opinion that the internal structure of teeth may be adaptive and that classification should therefore not be based entirely upon it. Despite this consideration, however, the results of a comparison of cochlodont, holocephalian, and ptyctodont teeth seems useful. The difference between holocephalian teeth and those of cochlodonts, although the latter fishes were apparently durophagous, should be kept in mind. The resemblance between the structure of ptyctodont and holocephalian teeth may be significant in combination with other evidence.

One should not leave a discussion of chimaerid toothplates without mentioning the problem of their origin. Their plate-like structure is unusual and has dictated comparisons between the Holocephali and other vertebrates like Dipnoi that also possess plate-like formations in the mouth. These comparisons founder, however, upon one point. The plates of lungfish, the teeth of most cochlodonts, and the pavement dentition of rays, all can be shown to be compounded of units which arise first as separate entities. In holocephalians no amalgamation of individual denticles is demonstrable. Even in the early embryos which Schauinsland studied there were no

indications of a fusion of teeth or tooth buds. It is possible that the Holocephali descended from forms whose teeth lost their discrete nature and that, as the group evolved, ontogenetic evidence of fusion was suppressed. Since it has not been demonstrated that all fossilized toothplates evolved through a compounding of individual units, however, it may be that holocephalian toothplates were derived from pre-existing integral structures. As antecedents of holocephalian toothplates, ptyctodont plates might be preferable to large cochlodont teeth produced through fusion.

In turning from the toothplates to the digestive tract, one reaches a series of structures whose evolutionary history is even harder to define. All the Holocephali show, beyond the mouth and pharynx, an esophagus which leads to the intestine directly, without the intervention of a differentiated stomach expansion. The obvious question—is the lack of a stomach a primitive or a degenerate character?—has found no sure answer. Since the stomachless condition is found in a number of unrelated fishes, one could argue that it represents a common type of degeneration which has occurred independently in several lines. On the other hand, the absence of a stomach in cyclostomes may be a remnant of the earliest vertebrate plan. At least one worker, Fahrenholz (1915), assumes that this is true in the case of the Holocephali. Since one answer seems as logical as the other, neither can be relied upon to carry much weight in the solution of the evolutionary problem.

The same may be said about the holocephalian spiral intestine. All the chimaerid fishes show an intrainstestinal fold which takes one slow turn throughout the greatest part of the intestinal tube and then makes two and a half tighter turns at the posterior end. The edge of the fold is free in the loosely coiled forepart and caught up in the center of the corkscrew turns at the end. This arrangement seems to be a combination of the "gerollte" type which Jacobshagen (1915) described as existing in a few sharks

and the "gedrehte" type which he declared to be much more common amongst the selachians. The peculiar nature of the spiral valve can be interpreted in either of two ways. Firstly, as Fee (1925) and Dean (1906) see it, the viscera of the chimaerid fishes, believed by them to be modified relatively late from sharks, have been crowded into a shortened body cavity. The stomach dilation fails to develop and "the intestinal valve, instead of undergoing the further spiral development of sharks, makes but a few turns (about four) . . ." (Fee, 1925: 179). The view of the valve arrangement as secondary, as set forth here, might be supported by Jacobshagen's contention that reduction in the intestinal fold always takes place from the anterior end. In fishes which bear a degenerate spiral valve or a vestigial one, the parts of it that remain are in the posterior region of the intestine. Secondly, the holocephalian valve might be held as primitive, especially in its histological structure. Evidence for this contention has been presented by Jacobshagen (1934), who has made a detailed comparative study of the spiral intestine in selachian, dipnoan, ganoid, and jawless fish. He points out that the valvular infolding in sharks includes only the mucosa and the muscularis mucosae. Since the ammocoetes larva shows inclusion of circular muscle as well, Jacobshagen suggests that the primitive fold was an indentation of the whole intestinal wall which lay within the enveloping serosa. Significantly, the holocephalians are the only fish that show portions of the main circular muscle of the intestine still included in the adult valvular fold. Of course, Jacobshagen's idea may be incorrect, and the inclusion of the muscle may not be a primitive condition in either animal.

As one advances to a consideration of the glands associated with the digestive tract, one finds less and less information available. Scammon, who has studied the selachian liver, reports in his account of it that "the histology of the adult elasmobranch

liver was first briefly described by Leydig from observations on *Chimaera*" (Scammon, 1915: 245). Since Scammon does not even think to distinguish the holocephalian from the selachian organ, it is apparent that their characteristics must be very much alike. Scammon holds that the elasmobranch liver differs from that of other vertebrates by its unique type of lobulation, its accumulation of fat within the hepatic cells, and its comparatively slight development of the bile duct system. It is impossible to decide whether these characteristics are peculiar to the shark line or whether they arose deep within the placoderm stock.

The holocephalian pancreas has apparently not been studied. Siwe, writing in 1926, does not mention the chimaerid structure in his paper on the comparative anatomy of that gland. The only other glandular organ associated with the digestive tract of the Holocephali that has received attention is an intraparietal mass of tubules located at the posterior end of the spiral valve. Citterio (1932) discusses this gland, first described by Leydig, suggesting that it might be homologous to the digitiform gland of selachians and more primitive in its intraparietal location.

Another structure which may have a selachian homology is the mass of lymphomyeloid tissue dorsal to the skin of the palate. Extant sharks and rays have a pair of structures, similar in their histology, built into the sides of the esophagus (Fahrenholz, 1915). The tissue itself seems of a like construction in the Holocephali and the selachians: both show several different types of myeloid cells set in a fibrous stroma which is highly vascular. Kolmer (1923) who examined the tissue in *Chimaera monstrosa* regarded it as hemopoietic. Its distribution in the Holocephali is singular. There is none in the esophageal wall, but it exists in a large mass not only over the palate but also within each orbit and in the ethmoid canal. The tissue masses are connected by strands which run through foramina from one area to another. There seems

to be a relatively small mass of it, isolated from the rest, within a pair of ventral channels in the pectoral girdle. Kolmer, impressed by the fact that much of this tissue was surrounded by cartilage, refers to it as "knockenmarkähnliche Gewebe." However, all of it seems to be external to the perichondrium. The presence of this tissue raises more questions than it answers. No one has dared to guess whether it is, in its present extent in the Holocephali, a specialization lately developed or another primitive vestige.

Conclusions from the nature of the digestive tract are difficult to draw. The Holocephali are extraordinary in the structure of their teeth, the lack of a stomach, the design of the intestinal valve, and the presence in association with the gut of unique masses of glandular and lymphomylod material. Examination of these characteristics, however, does not produce extensive evidence of value in solving the phylogenetic problem. Some clues may be gleaned, nevertheless. The greater resemblance between the internal structure of holocephalian and ptyctodont teeth than between those of holocephalians and coeliodonts suggests, if such similarities are at all significant, that there is more likelihood of a relationship between the Holocephali and the former than the latter group. The contrast between the integral structure of holocephalian toothplates and the tendency toward fusion of teeth which Moy-Thomas (1936) describes as being exhibited by the coeliodont *Helodus* makes it seem improbable that this type of coeliodont was ancestral to the Holocephali.

A hint of similarity to selachians lies in the likeness of the liver in the two groups of cartilaginous fishes. The affinities of the remaining soft parts of the digestive system of holocephalians defy analysis. It is impossible to determine whether the lack of a stomach and the minimal development of the spiral valve are primitive or secondary conditions. The evolution of the glandular mass at the posterior end of the intestine

and of the lymphomylod matter in the pharyngeal region is equally obscure. One must admit, then, that little can be derived from an analysis of the digestive organs to reinforce either the theory of a selachian or a non-selachian origin of the Holocephali.

CONCLUSION

The study of the venous system of *Chimaera colliciei* was undertaken in an attempt to clarify the evolutionary history of the Holocephali. The fishes of this group have been long regarded as an offshoot from the shark line and as such have been placed with selachians, bradyodonts, and batoids, in the class Chondrichthyes. The non-replacement of their toothplates resulted in their association with the bradyodonts, and through the work of Moy-Thomas (1936) the theory was established that they might have descended from a coeliodont of that group. Of late, however, Ørvig (1962) has argued that the Holocephali are more probably derived from a ptyctodont ancestor and so only distantly related to sharks.

In an effort to re-evaluate the position of the Holocephali, the anatomy of the venous system was examined for similarities and differences between it and that of other fishes. Undoubted resemblances to the selachian system were found in the presence and arrangement of sinuses and in the existence of a subcutaneous network of veins. The hepatic portal system, while not exactly like that of sharks, resembled the selachian system more nearly than that of bony fishes. The two main points of difference from selachians lay in the absence of the hepatic veins into the posterior cardinal sinuses. Further examination of the circulatory system brought forth no similarities to the bony fishes but a heart of the selachian type, and a unique arrangement of arteries in the head region. It was obvious from the study of the circulatory system that holocephalian structure agreed with that of bony fishes only in the lack of lateral abdominal veins, and that it bore

a much greater resemblance to the selachian type. The peculiarities of holocephalian vessel arrangement gave no clue as to their derivation. It was impossible to determine whether they represented modifications from the selachian plan or whether they had been inherited from a non-selachian source.

A review of the holocephalian nervous, skeletal, muscular, urogenital, and digestive systems was made in the search for characteristics whose derivation could be more clearly interpreted. Since each system displayed distinct differences from the comparable system of bony fish, and the similarities to selachian structure were often marked, the degree and the implications of the resemblance to selachians became the focal problem.

A strong similarity between holocephalian and selachian structure allows the possibility of the origin of the former from the latter group but does not necessitate it. The possession of similar structures might also have occurred through their inheritance from a common ancestor at a lower level of the vertebrate line. In the case of a single structure, its presence may be the result of parallel evolution. The existence of characters which seem unlikely to be derived from selachian structures or of those which seem more primitive than their homologues in sharks might be less equivocal. If it can be shown that a structure is basically unlike its selachian counterpart or that it is not a secondary simplification of a form which exists in a more specialized state in sharks, one could conclude that the Holocephali should logically be traced back to placoderm stock by an independent line rather than to an early shark group.

The review of the nervous system revealed likenesses to selachians in the arrangement of the autonomic fibers and the anatomy of the sense organs and posterior regions of the brain. Although the unusual form of the telencephalon could have originated as a modification from the selachian plan, it does not appear likely that

the structure of the pallium itself or the simple arrangement of the cranial nerves could have been so derived. It appears doubtful too, that the pattern of the sensory canals came from a selachian source.

The fact that the skeleton of both holocephalians and sharks is completely cartilaginous was once thought to be indicative of close relationship, but it has become apparent that that conclusion is not the only possible one. Since it seems, now, that a transition from bone to cartilage occurred in several vertebrate lines, one must allow that the cartilaginous skeletons of sharks and holocephalians may have developed independently. If one can look beyond the similarity of the skeletal material, holocephalians can be seen to have several skeletal characters that would be difficult to derive from early sharks. Their form of autostyly is distinctive. Although it appears that autostyly has developed several times among vertebrates, it is hard to believe that the arrangement in the Holocephali could be a modification of selachian structure. If it were, one would expect to find a longer palatoquadrate element rather than a short one with a process extending postero-dorsally in finger-like fashion to reach the otic region. Also, the hyoid would be expected to show some sign of its former involvement in the jaw suspension. In holocephalians it does not, being to all appearances exactly like the succeeding arches even in its dorsal part. In addition to the difference of the palatoquadrate and hyoid elements from the shark type, the presence of elaborate labial and rostral cartilages and the general proportions of the skull, with its short otic and steeply sloped ethmoid areas, distinguish holocephalians from early sharks.

A study of the muscular system produces less that is clearly significant. The similarity of the musculature of fishes generally and the difficulty of ascertaining homologues are obstacles to meaningful analysis. Peculiarities in holocephalian axial, appendicular, and branchial muscles are appar-

ent, but there is nothing to indicate whether they were or were not derived from the selachian plan. There seems to be no sure ground for denying that they could have been.

The urogenital system of holocephalians resembles that of sharks very closely in the nature of kidneys, the gonads, the accessory ducts, and the interrelationship between those structures. Because that interrelationship is characteristic of most extant vertebrates (bony fish are the cardinal exception), it is possible to interpret the arrangement as one which was widespread among early gnathostomes and so obviate the necessity of deriving the holocephalian system from a specifically selachian source. If one is free to seek its forerunner in a wide variety of early vertebrate groups, one might consider the ptyctodonts as having had a system which could have been ancestral to the holocephalian type. Although no evidence of soft organs remains, it seems that ptyctodonts may have had, associated with the reproductive system, accessory claspers similar to those of holocephalians. No trace of those structures appears in any other fossil group.

The digestive system of the Holocephali is unlike that of selachians in its lack of a stomach and poor development of the spiral valve. Among the soft organs, the liver is the only structure which bears a striking resemblance to its selachian counterpart. While the evolutionary history of the soft parts of the digestive system is not clear, the holocephalian toothplates, which show no evidence of having developed through a fusion of separate teeth, seem not to be derived from any known shark structures.

The general conclusion to be drawn from this study is that, although similarities between holocephalians and selachians are numerous, holocephalians possess certain characteristics which suggest that these fishes evolved from other than a selachian stock. The existence in sharks and holocephalians of like structures does not con-

tradict this hypothesis, since such structures may have been carried over from a common ancestor or developed convergently. Even the derivation of the Holocephali from the bradyodont sharks can be questioned. Although the cochliodont *Helodus* shows, according to Moy-Thomas, a number of similarities to holocephalians, the teeth of that fish show a tendency toward fusion of which there is no hint in the Holocephali. *Helodus* was apparently autostylic, as are the holocephalians, but autostyly has arisen repeatedly in vertebrate groups and cannot be considered as weighty evidence in favor of the holocephalian-cochliodont relationship. There is as good, or better, evidence in favor of a relationship between holocephalians and ptyctodonts. Although the ptyctodont palatoquadrate was not fused to the cranium, the toothplates appear to have been integral structures, and the body form, with the large, short head, was similar to that of holocephalians. If one will concede that the dermal skeleton of the ptyctodonts could have disappeared as the evolution of the group continued, then the presence of labial cartilages, rostral processes, anterior and pelvic claspers, a synarcual, and a dorsal fin supported by radials posterior to the dorsal spine, stand forth as a substantial and therefore possibly significant number of characteristics suggesting linkage between the ptyctodont and holocephalian lines.

In sum, one may assume from available evidence that holocephalians are not derived from selachians or bradyodonts but have evolved along an independent line. However, anatomical similarities between extant holocephalians and selachians which set both groups apart from the bony fishes suggest that these cartilaginous forms shared a common ancestor. This ancestral stock must have existed at the placoderm level or even earlier among unknown antecedent forms. Although the specific group of placoderms from which sharks originated is unknown, the ptyctodonts may represent the root of the holocephalian line.

ACKNOWLEDGMENTS

I want to express my gratitude to Dr. Alfred S. Romer of Harvard University for the guidance and encouragement that he has given me throughout my research and the preparation of this paper. I am indebted, also, to Dr. Richard Snyder of the University of Washington and to Dr. Norman J. Wilimovsky of the University of British Columbia through whose efforts I obtained the specimens of *Chimaera coliei* that I used. Instruction in the technique of latex-injection was given me by Dr. Richard Thorington who was, at the time, a graduate student at the Harvard Biological Laboratories. Mrs. Myvanwy Dick allowed me to preserve and store my fishes in the Fish Department of the Museum of Comparative Zoology and was kind enough to lend me a specimen of *Callorhynchus*. The list of people who answered my letters of inquiry is very long. I owe thanks especially to Dr. D. L. Gamble of Ward's and to Mr. Thomas E. Powell, Jr. of Carolina Biological Supply Company who sent advice about injecting frozen-and-thawed material. Lastly, I should like to thank Dr. David G. Stahl who encouraged me to undertake this work and whose patience and good will enabled me to finish it.

REFERENCES CITED

- ALLEN, W. F. 1905. The blood vascular system of the Loricati, the mail-cheeked fishes. *Proc. Washington Acad. Sci.*, **7**: 27-157.
- ALLIS, E. P. 1912. The branchial, pseudobranchial, and carotid arteries in *Chimaera coliei*. *Anat. Anz.*, **42**: 10-18.
- . 1916. The so-called mandibular artery and the persisting remnant of the mandibular aortic arch in the adult selachian. *J. Morph.*, **27**: 99-118.
- . 1917. The prechordal portion of the chondrocranium of *Chimaera coliei*. *Proc. Zool. Soc. London*, 1917: 105-143.
- . 1926. On the homologies of the prechordal portions of the skull of the Holocephali. *J. Anat.*, **60**: 335-340.
- BÄCKSTROM, K. 1924. Contributions to the fore-brain morphology in selachians. *Acta Zool.*, **5**: 123-240.
- BARGMANN, W. 1933. Die Zahnplatten von *Chimaera monstrosa*. *Z. Zellforsch.*, **19**(3): 537-561.
- BORCEA, J. 1906. Recherches sur le système urogenital des elasmobranches. *Arch. Zool. (Paris)*, Sér. 4, **4**: 199-484.
- BRAUS, H. 1898. Über die Innervation der paarigen Extremitäten bei Selachiem, Holocephalen, und Dipnoen. Ein Beitrag zur Gliedmassenfrage. *Jena. Z. Med.*, **31**: 239-468.
- BRETTNACHER, H. 1939. Aufbau und Struktur der Holocephalenzähne. *Z. Mikr. Anat. Forsch.*, **46**: 584-616.
- BURLEND, T. H. 1910. The urogenital organs of *Chimaera monstrosa*. *Proc. Zool. Soc. London*, 1910: 510-534.
- CITTERIO, V. 1932. Ricerche sul canale digerente di *Chimaera monstrosa*. *Atti Soc. Ital. Milano*, **71**: 93-118.
- COLE, F. J. 1896. The cranial nerves of *Chimaera monstrosa*. *Trans. Roy. Soc. Edinburgh*, **38**: 49-56.
- COLE, F. J. AND W. J. DAKIN. 1906. Further observations on the cranial nerves of *Chimaera*. *Anat. Anz.*, **28**: 595-599.
- DANIEL, J. R. 1934. The elasmobranch fishes. Berkeley, 334 pp.
- DAVIDOFF, M. v. 1879. Beiträge zur vergleichenden Anatomie der hinteren Gliedmasse der Fische. I. Haie, *Chimaera* und Ganoidei chondrostei. *Morph. Jahrb.*, **5**: 450-520.
- DEAN, B. 1895. Fishes living and fossil. Macmillan, New York, 300 pp.
- . 1904. In the matter of the Permian fish *Menaspis*. *Amer. Geol.*, **34**: 49-53.
- . 1906. Chimaeroid fishes and their development. Carnegie Inst. Washington, Pub. No. **32**, 172 pp.
- . 1909. Studies on fossil fishes (sharks, chimaeroids, arthrodires). *Mem. Amer. Mus. Nat. Hist.*, **9**: 207-287.
- DEBEER, G. R. AND J. A. MOY-THOMAS. 1935. On the skull of the Holocephali. *Phil. Trans. Roy. Soc. London*, B **224**: 287-312.
- EDGEWORTH, F. H. 1935. The cranial muscles of vertebrates. Cambridge, 300 pp.
- FAHRENHOLZ, C. 1915. Über die Verbreitung von Zahnbildungen und Sinnesorganen in Vorderdarm der Selachier und ihre phylogenetische Beurteilung. *Jena. Z. Naturwiss.*, **53**: 389-444.
- FEE, A. R. 1925. The histology of the colon and its contained spiral valve of the Pacific Coast dog-fish (*Squalus sucklii*) with an investigation of the phylogeny of the intestinal valve. *Proc. Trans. Roy. Soc. Canada*, Sect. V, **19**: 169-193.
- FÜRBRINGER, M. 1897. Über die spino-occipitalen Nerven der Selachier und Holocephalen

- und ihre vergleichende Morphologie. In: Festschr. 70 Geburtstag C. Gegenbaur, Leipzig, **3**: 349-788.
- GARMAN, S. 1888. On the lateral canal system of the Selachia and Holocephalia. *Bull. Mus. Comp. Zool.*, **17**: 57-119.
- . 1904. The chimaeroids, especially *Rhinochimaera* and its allies. *Bull. Mus. Comp. Zool.*, **41**: 243-272.
- GROSS, W. 1957. Mundzähne und Hautzähne der Acanthodier und Arthrodiren. *Paleontographica*, **109**(A): 1-40.
- HOLMGREN, N. 1922. Points of view concerning forebrain morphology in lower vertebrates. *J. Comp. Neur.*, **34**: 391-440.
- . 1942a. General morphology of the lateral sensory line system of the head in fish. *K. Svenska Vetenskaps-Acad. Handl., Ser. 3*, **20**(1): 1-46.
- . 1942b. Studies on the head of fishes, an embryological, morphological, and phylogenetical study. 3: The phylogeny of elasmobranch fishes. *Acta Zool.*, **23**: 129-261.
- HOLMGREN, N. AND C. J. VAN DER HORST. 1925. Contributions to the morphology of the brain of *Ceratodus*. *Acta Zool.*, **6**: 59-165.
- HUBRECHT, A. A. W. 1877. Beiträge zur Kenntniss des Kopfskeletts der Holocephalen. *Niederl. Archiv. f. Zool.*, **3**: 255-276.
- HYMAN, L. H. 1942. Comparative vertebrate anatomy. 2nd ed., Chicago, 544 pp.
- HYRTL, J. 1853. Ueber weibliche Oviducte bei männlichen Chimaeren, und eine männliche Vesicula seminalis bei Weibchen. *Sitzungsber. K. Akad. Wiss. (Vienna)*, **11**(5): 1078-1087.
- JACOBSEN, E. 1915. Untersuchungen über das Darmsystem der Fische und Dipnoer. *Jena. Z. Naturwiss.*, **53**: 445-556.
- . 1934. Das Problem des Spiraldarms. *Morphol. Jahrb.*, **73**: 392-445.
- . 1941. Grundlinien einer vergleichenden Anatomie des Zahnbeines und der Zähne niederer Wirbeltiere. *Z. Mikros. Anat. Forsch.*, **49**: 225-272.
- JOHNSTON, J. B. 1910. A note on the forebrain of *Chimaera*. *Anat. Anz.*, **36**: 233-242.
- KAPPERS, C. U. A. 1912. The arrangement of the motor nuclei in *Chimaera monstrosa* compared with other fishes. *Proc. K. Akad. Wetensch.*, **14**: 1176-1180.
- KAPPERS, C. U. A. AND F. W. CARPENTIER. 1911. Das Gehirn von *Chimaera monstrosa*. *Folia Neurobiologica*, **5**: 127-160.
- KAPPERS, C. U. A., G. C. HUBER, AND E. C. CROSBY. 1936. The comparative anatomy of the nervous system of vertebrates. 3 Vols., New York, 1845 pp.
- KESTEVEN, H. L. 1933. The anatomy of the head of *Callorhynchus antarcticus*. *J. Anat.*, **67**: 443-474.
- . 1942-1943. The evolution of the skull and the cephalic muscles. Part I. The fishes. *Mem. Aus. Mus.*, **8**: 1-132.
- KOLMER, W. 1923. Über das Vorkommen eines knochenmarkähnlichen Gewebes bei einem Selachier (Knorpelmark bei *Chimaera monstrosa*). *Anat. Anz.*, **56**: 529-534.
- LANKESTER, E. R. 1878. On the hearts of *Ceratodus*, *Protopterus*, and *Chimaera*. *Trans. Zool. Soc. London*, **10**: 493-505.
- LEIGH-SHARPE, W. H. 1920-1926. The comparative morphology of the secondary sexual characters of elasmobranch fishes. *J. Morph.*, **34**: 245-265; **35**: 359-380; **36**: 221-243; **39**: 558-577; **42**: 307-308.
- LEYDIG, F. 1851. Zur Anatomie und Histologie der *Chimaera monstrosa*. *Arch. Anat. Physiol.*, 1851: 241-271.
- LUTHER, A. 1909. Beiträge zur Kenntnis von Muskulatur und Skelett des Kopfes des Haies *Stegostoma tigrinum* Gm. und der Holocephalen. *Acta Soc. Sci. Fennicae*, **37**: 1-60.
- MARPLES, B. J. 1936. The blood vascular system of the elasmobranch fish *Squatina squatina* (Linné). *Trans. Roy. Soc. Edinburgh*, **58**: 817-840.
- MAURER, FR. 1912. Die ventrale Rumpfmuskulatur der Fische. *Jena. Z. Naturwiss.*, **49**: 1-118.
- MOY-THOMAS, J. A. 1936. On the structure and affinities of the Carboniferous coelodont *Helodus simplex*. *Geol. Mag.*, **73**: 488-503.
- NICOL, J. A. C. 1950. The autonomic nervous system of the chimaeroid fish, *Hydrolagus collicii*. *Quart. J. Micros. Sci.*, **91**: 379-400.
- NIELSEN, E. 1932. Permo-carboniferous fishes from East Greenland. *Medd. om Grønland*, **92**(3): 1-63.
- . 1952. On new or little-known Edestidae from the Permian and Triassic of East Greenland. *Medd. om Grønland*, **144**(5): 1-55.
- O'DONOGHUE, C. H. 1914. Notes on the circulatory system of elasmobranchs. I. The venous system of the dogfish (*Scyllium canicula*). *Proc. Zool. Soc. London*, 1914: 435-455.
- ØRVIG, T. 1951. Histologic studies of placoderms and fossil elasmobranchs. I. The endoskeleton with remarks on the hard tissues of lower vertebrates in general. *K. Svenska Vetenskap.-Akad., Ark. Zool., Ser. 2*, **2**(2): 321-454.
- . 1957. Notes on some Paleozoic lower vertebrates from Spitzbergen and North America. *Norsk Geol. Tidsskr.*, **37**(3-4): 285-353.
- . 1962. Y a-t-il une relation directe entre les arthrodires ptyctodontides et les holocephales? *Problèmes Actuels de la Paléontologie*, Centre Nat. Recher. Sci., No. **104**: 49-61.

- PANDER, C. H. 1858. Über die Ctenodipterinen des devonischen Systems. St. Petersburg, 65 pp.
- PARKER, T. J. 1886. On the blood vessels of *Mustelus antarcticus*. Phil. Trans. Roy. Soc. London, Ser. B, **177**: 685-731.
- PATTERSON, C. 1965. The phylogeny of the chimaeroids. Phil. Trans. Roy. Soc. London, Ser. B, **249**: 101-219.
- PRASAD, R. R. 1948. Observation on the nidamental glands of *Hydrolagus collicii*, *Raja rhina* and *Platyrhinoidis triseriatus*. Copeia, No. 1: 54-57.
- RABINERSON, A. 1925. Beiträge zur vergleichenden Anatomie der Wirbelsäule der Knorpelfische. Anat. Anz., **59**: 433-454.
- RADINSKY, L. 1961. Tooth histology as a taxonomic criterion for cartilaginous fishes. J. Morphol., **109**: 73-92.
- REDEKE, H. C. 1898. Onderzoekingen betreffende het Urogenitaalsysteem der Selachiers en Holocephalen. Amsterdam, 85 pp.
- REESE, A. M. 1910. The lateral line system of *Chimaera collicii*. J. Exp. Zool., **9**: 349-370.
- ROMER, A. S. 1964. The braincase of the Paleozoic elasmobranch *Tamiodontis*. Bull. Mus. Comp. Zool., **131**(4): 89-105.
- SCAMMON, R. E. 1915. The histogenesis of selachian liver. Amer. J. Anat., **17**: 245-315.
- SCHIAUINSLAND, H. H. 1903. Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere, I., *Sphenodon*, *Callorhynchus*, *Chamaeleo*. Zoologica, **39**: 1-98.
- SHANN, E. W. 1919. The comparative myology of the shoulder girdle and pectoral fin of fishes. Trans. Roy. Soc. Edinburgh, **52**: 531-570; continued in Proc. Zool. Soc. London, 1924: 195-215.
- SIWE, S. A. 1926. Pancreasstudien. Morphol. Jahrb., **57**: 84-307.
- STENSIÖ, E. 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. K. Svenska Vetenskaps-Akad. Handl., Ser. 3, **24**(3): 1-195.
- . 1963. Anatomical studies on the arthrodontan head. Part I. K. Svenska Vetenskaps-Akad. Handl., **9**(2): 1-419.
- VAN DEN BROEK, A. J. P. 1938. Gonaden und Ausführungsgänge. In: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 6: 1-154.
- VAN GELDEREN, CHR. 1938. Venensystem, mit einem Anhang über den Dotter- und Plazentarkreislauf. In: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 6: 685-744.
- VAN DER HORST, C. I. 1934. Spinalnerven. In: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 2: 505-540.
- VAN OORDT, G. J. 1938. Besondere Morphologie der Harnorgane der Wirbeltiere. In: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 5: 727-836.
- VETTER, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermuskeln der Fische. II Teil. Jena. Z. Naturwiss., **12**: 431-550.
- WATSON, D. M. S. 1938. A pytyodont from the middle Old Red Sandstone of Scotland. Trans. Roy. Soc. Edinburgh, **59**(2): 397-410.
- WILDER, B. 1877. On the brain of *Chimaera monstrosa*. Proc. Acad. Nat. Sci. Philadelphia, 1877: 219-250.

(Received 27 September, 1965.)

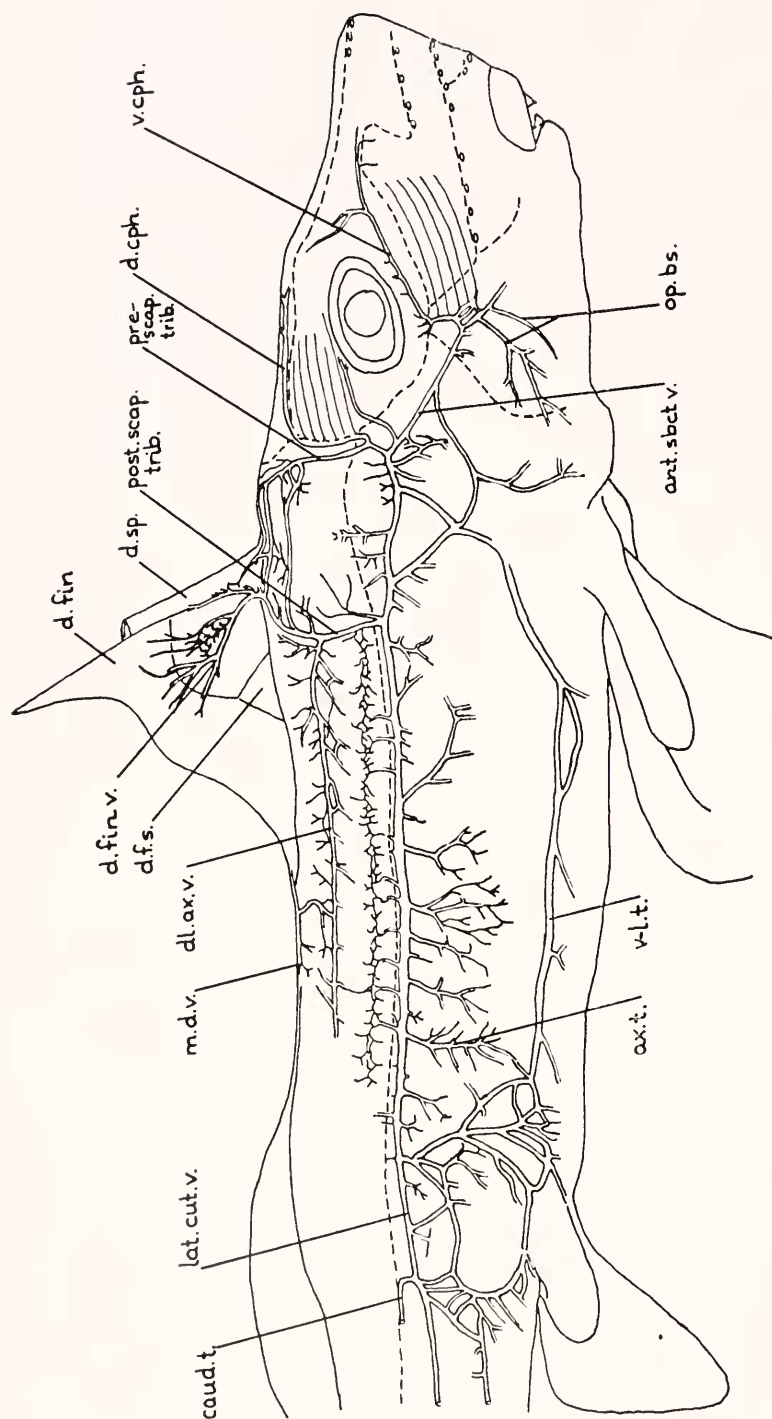


Plate 1. The subcutaneous veins of *Chimaera colliciei*. Lateral view. $\times 0.5$. ant.sbct.v., Anterior subcutaneous vein; ax.t., axial tributary; caud.t., caudal tributary; d.cph., dorsal cephalic branch; d.fin, dorsal fin; d.fin v., dorsal fin vein; d.f.s., dorsal fin sinus; dl.ax.v., dorso-lateral axial vein; d.sp., dorsal spine; lat.cut.v., lateral cutaneous vein; m.d.v., median dorsal vein; op.bs., opercular branches; post.scap.trib., postscapular tributary; pre.scap.trib., prescapular tributary; v.cph., ventral cephalic branch; v.l.t., ventro-lateral tributary.

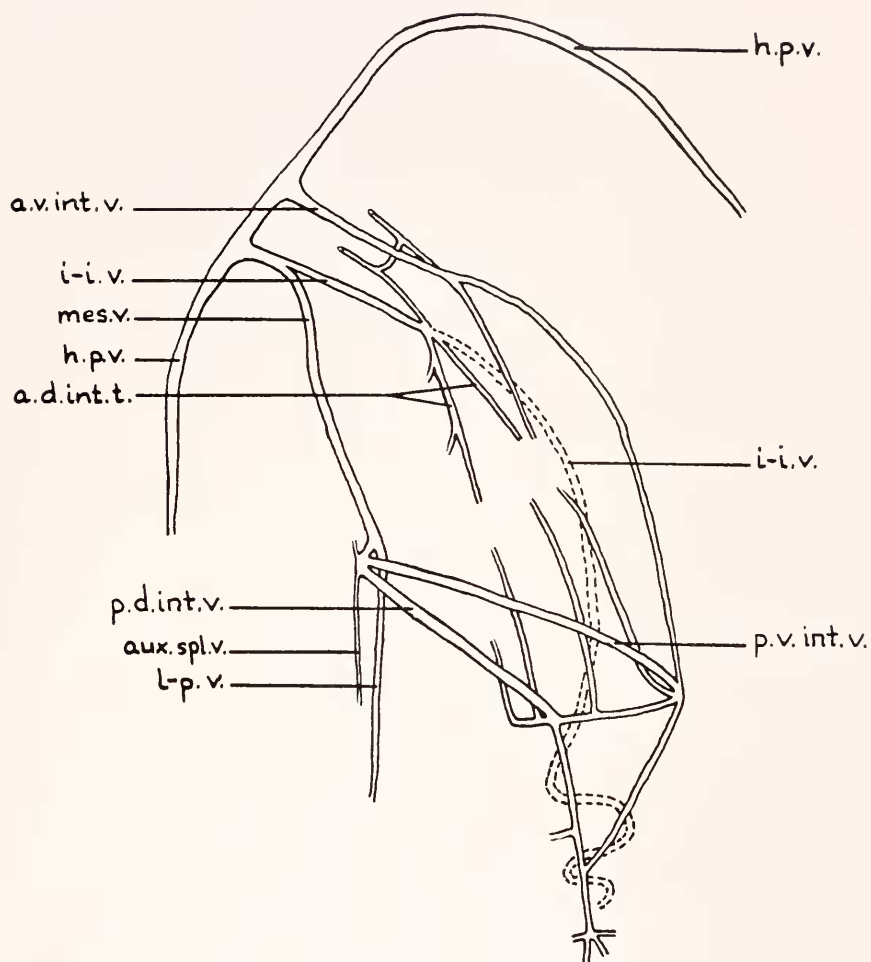


Plate 2. The hepatic portal system of *Chimaera calliei*. Diagrammatic view. $\times 0.75$. a.d.int.t., Anterior dorsal intestinal tributary; aux. spl.v., auxiliary splenic vein; a.v.int.v., anterior ventral intestinal vein; h.p.v., hepatic portal vein; i-i.v., intra-intestinal vein; l-p.v., liena-pancreatic vein; mes.v., mesenteric vein; p.d.int.v., posterior dorsal intestinal vein; p.v.int.v., posterior ventral intestinal vein.

Plate 3. The systemic and renal portal veins of *Chimaera colliei*. Diagrammatic view. $\times 0.5$. a.br.v., Anterior brachial vein; ant.card., anterior cardinal sinus; ant.cer.a., anterior tributary of the anterior cerebral vein; ant.cer.p., posterior tributary of the anterior cerebral vein; ant.sbct.v., anterior subcutaneous vein; br.s., brachial sinus; br.s.mid-v.ext., mid-ventral extension of brachial sinus; caud.v., caudal vein; eth.v., ethmoidal vein; fem.v., femoral vein; h.v., hepatic vein; inf.jug.v., inferior jugular vein; il.v., iliac vein; lat.cut.v., lateral cutaneous vein; m-f.v., maxillo-facial vein; a-n.v., orbito-nasal vein; orb.s., orbital sinus; av.s., aviducal sinus; par.v., parietal vein; p.br.v., posterior brachial vein; post.card., posterior cardinal sinus; post.card.mid-v.ext., mid-ventral extension of posterior cardinal sinus; post.cer.v., posterior cerebral vein; postorb.v., postorbital vein; preorb.v., preorbital vein; prescap.t., prescapular tributary; rect.trib., rectal tributary; rn.v., renal vein; r.p.v., renal portal vein; sbsc.s., subscapular sinus; sbsc.trib., subscapular tributary; s.v., sinus venosus; v-a.par.v., ventro-anterior parietal vein; v-p.par.v., ventro-posterior parietal vein.

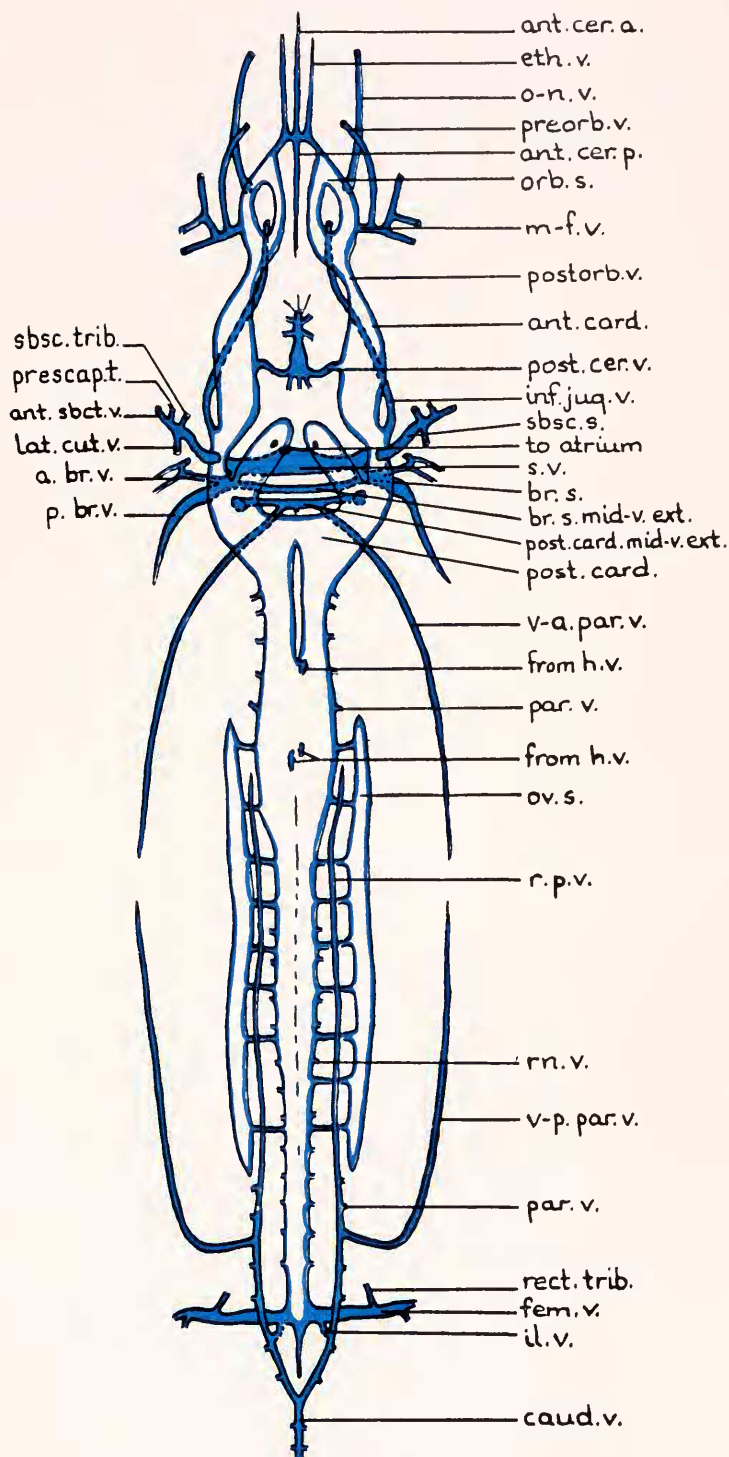
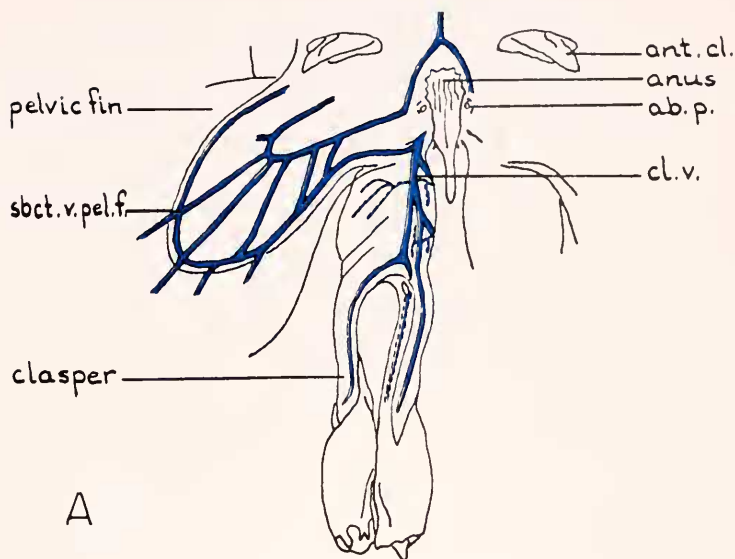


Plate 4. A, The subcutaneous veins of the clasper and pelvic fin. Ventral view. $\times 1$. B, The heart and vessels of the hypobranchial region. Ventral view. Caracomandibularis muscle and right half of pectoral girdle removed. $\times 1$. *ab.p.*, Abdominal pore; *aff.brn.a.*, afferent branchial artery; *ant.cl.*, anterior clasper; *br.a.*, brachial artery; *br.n.*, brachial nerve; *br.s.*, brachial sinus; *c.a.*, conus arteriosus; *c-brn.m.*, caracabbranchialis muscle; *c-h.m.*, caracohyoideus muscle; *cl.v.*, clasper vein; *c-m.m.*, caracomandibularis muscle; *com.card.*, common cardinal vein; *cor.c.*, coracoid cartilage; *hy.c.*, hyoid cartilage; *hyp.m.*, hypaxial muscle; *hypobr.n.*, hypobranchial nerve; *inf.jug.v.*, inferior jugular vein; *mand.c.*, mandibular cartilage; *m.w.g.c.*, medial wall of gill chamber; *pect.f.*, pectoral fin; *post.card.*, posterior cardinal sinus; *sbct.v.pel.f.*, subcutaneous veins of pelvic fin; *s.v.*, sinus venosus; *trib.inf.jug.*, inferior jugular tributary; *v.a.*, ventral aorta; *x*, fine vein accompanying ventral aorta.



A

B

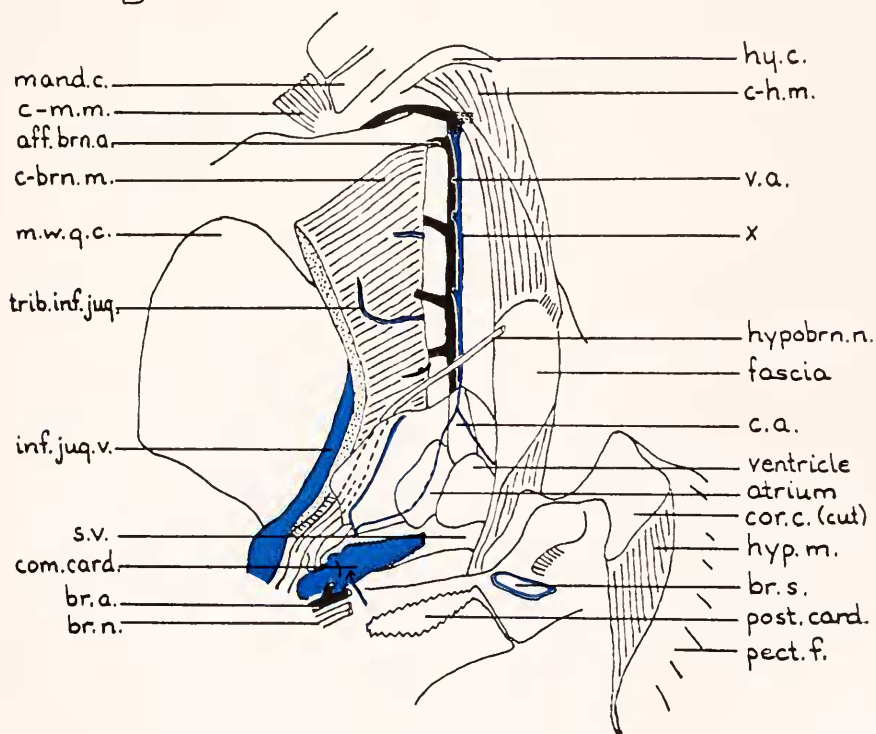


Plate 5. A, Origin of right inferior jugular vein, showing drainage of tissues immediately posterior to mandible. Ventral view. Coracamandibularis muscle cut and deflected toward midline. $\times 1$. B, The brachial veins. Postero-dorsal view of right pectoral fin, proximal region. $\times 1$. C, The systemic veins entering the sinus venosus. Diagrammatic view. $\times 0.5$. D, The anterior cerebral vein and its tributaries. Lateral view. Cartilage removed to show ethmoid and cranial cavities. $\times 1$. a.br.v., Anterior brachial vein; ant.card., anterior cardinal sinus; ant.cer.a., anterior tributary of the anterior cerebral vein; ant.cer.p., posterior tributary of the anterior cerebral vein; ant.cer.v., anterior cerebral vein; ant.v.const.m., anterior ventral constrictor muscle; a-v., antero-ventral; br.a., brachial artery; br.s., brachial sinus; cart., cartilage; cbl., cerebellum; cer.a., cerebral artery; c-m.m., coracamandibularis muscle; cam.card., common cardinal vein; ent.arb.s., entrance to orbital sinus; ep., epiphysis; eth.v., ethmoidal vein; hyp.m., hypaxial muscle; inf.jug.v., inferior jugular vein; int.hy.m., interhyoideus muscle; int.orb.sept., interorbital septum; lev.m., levator muscle; lig., ligament; lym., lymphomyeloid tissue; mand.c., mandibular cartilage; n.cap., nasal capsule; nas., nostril; a-n.v., orbita-nasal vein; opt.a., optic artery; opt.l., optic lobe; p.br.v., posterior brachial vein; pect.f., pectoral fin; pect.gir., pectoral girdle; post.card., posterior cardinal sinus; psb.a., pseudobranchial artery; sbsc.s., subscapular sinus; scap., scapula; sp.n., spinal nerve; sup.aph.n., superficial ophthalmic nerve; s.v., sinus venosus; tel., telencephalon; thy.gld., thyroid gland; tr.int.m., trapezius internus muscle; v.const.m., ventral constrictor muscle; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; X, vagus nerve.

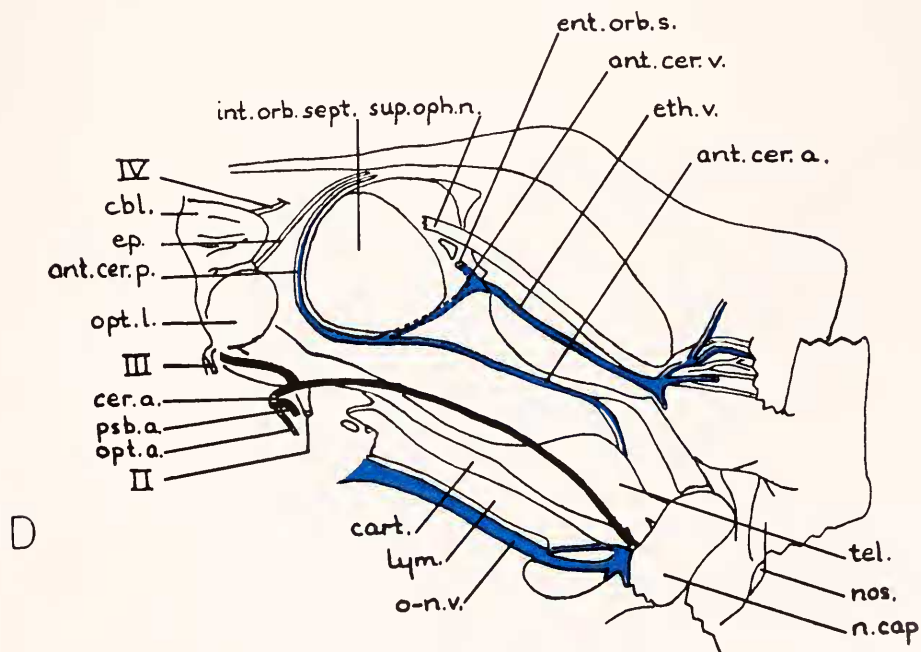
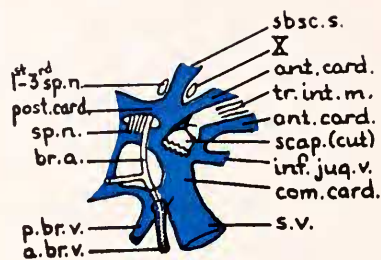
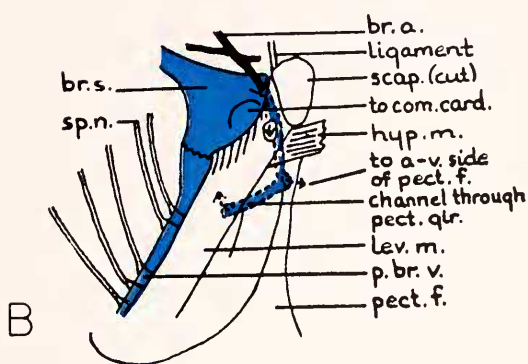
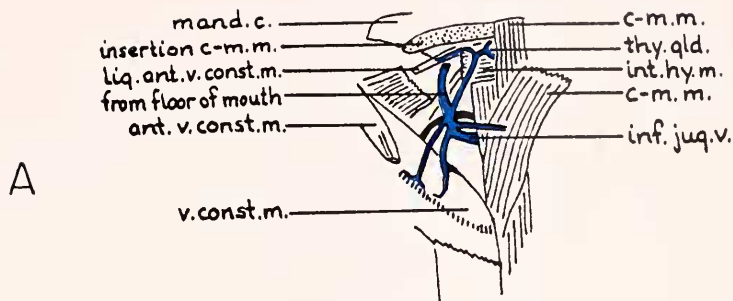
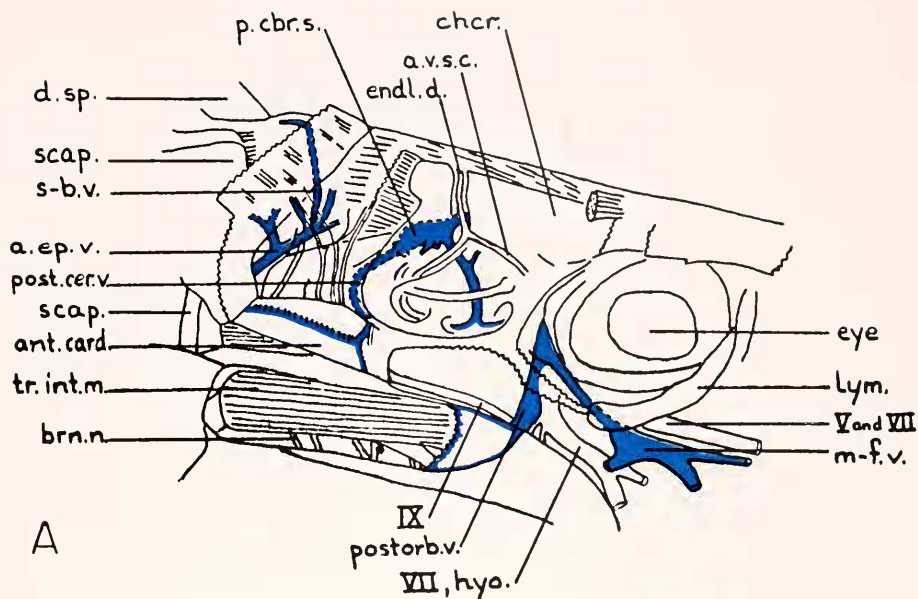


Plate 6. A, Systemic veins and related structures in the postero-dorsal region of the head. Lateral view. $\times 1$. B, Veins draining dorsal region of trunk. Lateral view. Epaxial muscles cut and partially removed. Scapular cartilage cut and deflected ventrally. $\times 1$. *a.ep.v.*, Anterior epaxial vein; *ant.card.*, anterior cardinal sinus; *a.v.s.c.*, anterior vertical semicircular canal; *brn.n.*, branchial nerve; *chcr.*, chondrocranium; *com.card.*, common cardinal vein; *d.const.m.*, dorsal constrictor muscle; *d.f.s.*, dorsal fin sinus; *d.sp.*, dorsal spine; *endl.d.*, endolymphatic duct; *ep.m.*, epaxial muscle; *lat.cut.v.*, lateral cutaneous vein; *lym.*, lymphomyeloid tissue; *m.d.v.*, median dorsal vein; *m-f.v.*, maxillo-facial vein; *ot.cap.*, otic capsule; *p.cbr.s.*, posterior cerebral sinus; *post.card.*, posterior cardinal sinus; *post.cer.v.*, posterior cerebral vein; *postorb.v.*, postorbital vein; *post.scap.trib.*, postscapular tributary; *sbsc.trib.*, subscapular tributary; *s-b.v.*, spino-basal vein; *scap.*, scapula; *sp.n.*, spinal nerve; *tr.int.m.*, trapezius internus muscle; V, trigeminal nerve; VII, facial nerve; VII, *hya.*, hyomandibular branch of facial nerve; IX, glossopharyngeal nerve; X, vagus nerve.



B

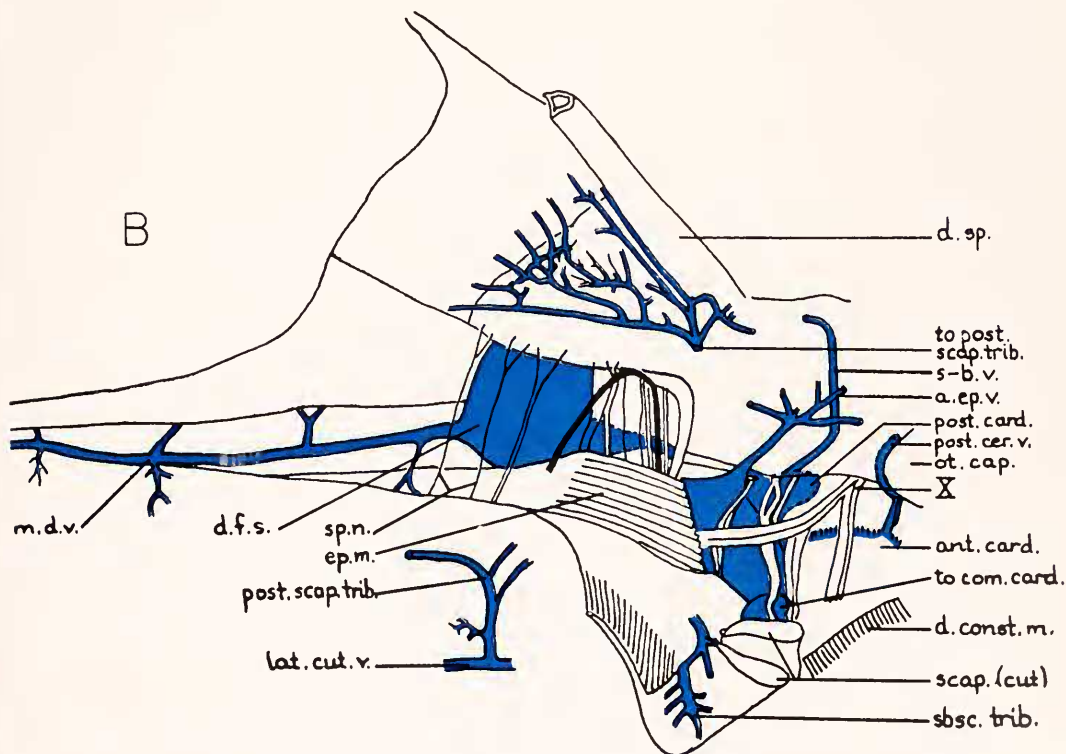


Plate 7. A, The maxillo-facial vein and its tributaries. Lateral view. Lower portion of adductor mandibulae muscle removed. $\times 1$. B, Deep veins associated with lymphomyeloid tissue dorsal to mouth cavity. Lateral view. Palatoquadrate cartilage cut and partially removed. $\times 1$. C, The femoral vein. Lateral view. Right side. $\times 0.75$. *cart.*, Cartilage; *d.lab.v.*, deep labial vein; *eff.rn.v.*, efferent renal vein; *ex.ov.op.*, external oviducal opening; *fem.a.*, femoral artery; *fem.v.*, femoral vein; *hy.c.*, hyoid cartilage; *lab.cart.*, labial cartilage; *lab.s.*, labial sinus; *lym.*, lymphomyeloid tissue; *mand.art.*, mandibular articulation; *m-f.v.*, maxillo-facial vein; *m.tp.*, mandibular toothplate; *n.cap.*, nasal capsule; *a-n.v.*, orbito-nasal vein; *orb.s.*, orbital sinus; *ov.s.*, oviducal sinus; *pel.gir.*, pelvic girdle; *post.card.*, posterior cardinal sinus; *postarb.v.*, postorbital vein; *pq.*, palatoquadrate; *preorb.m.*, preorbitalis muscle; *preorb.v.*, preorbital vein; *psb.a.*, pseudobranchial artery; *rect.trib.*, rectal tributary; *r.p.v.*, renal portal vein; *sam.*, samentasche; *v.const.m.*, ventral constrictor muscle; *v.tp.*, vomerine toothplate; *y*, hyoid tributary; *z*, possible venous pathways; *V*, trigeminal nerve; *VII*, facial nerve; *VII,hyo.*, hyomandibular branch of facial nerve; *VII,pal.*, palatine branch of facial nerve.

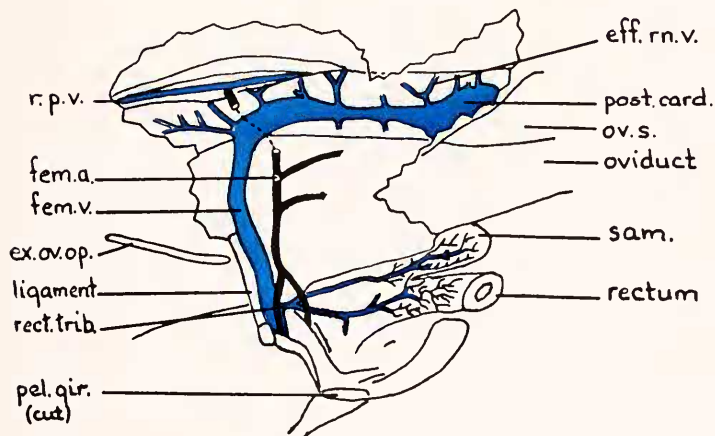
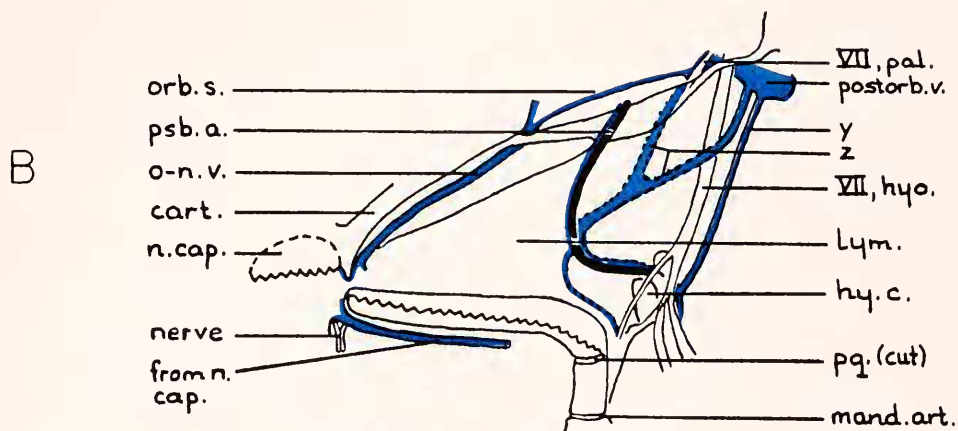
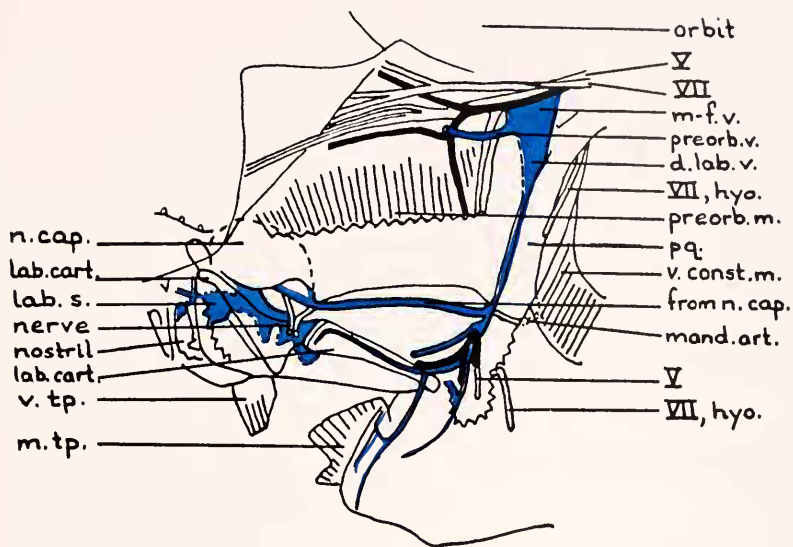




Plate 8. A, The renal portal vein. Lateral view. Left side. $\times 1$. B, The hepatic portal system. Dorsal view. $\times 1$. a.d.int.t., anterior dorsal intestinal tributary; aff.rn.v., afferent renal vein; a.v.int.v., anterior ventral intestinal vein; b.d., bile duct; esaph., esophagus; fem.a., femoral artery; fem.v., femoral vein; g.b., gall bladder; h.p.v., hepatic portal vein; hyp.m., hypaxial muscle; i-i.a., intra-intestinal artery; i-i.v., intra-intestinal vein; il.v., iliac vein; k., kidney; mes., mesentery; mes.v., mesenteric vein; av.s., aviducal sinus; pan., pancreas; pan.d., pancreatic duct; par.v., parietal vein; p.d.int.v., posterior dorsal intestinal vein; pel.gir., pelvic girdle; p.mes.a., posterior mesenteric artery; post.card., posterior cardinal sinus; p.v.int.v., posterior ventral intestinal vein; r.p.v., renal portal vein; spl., spleen.

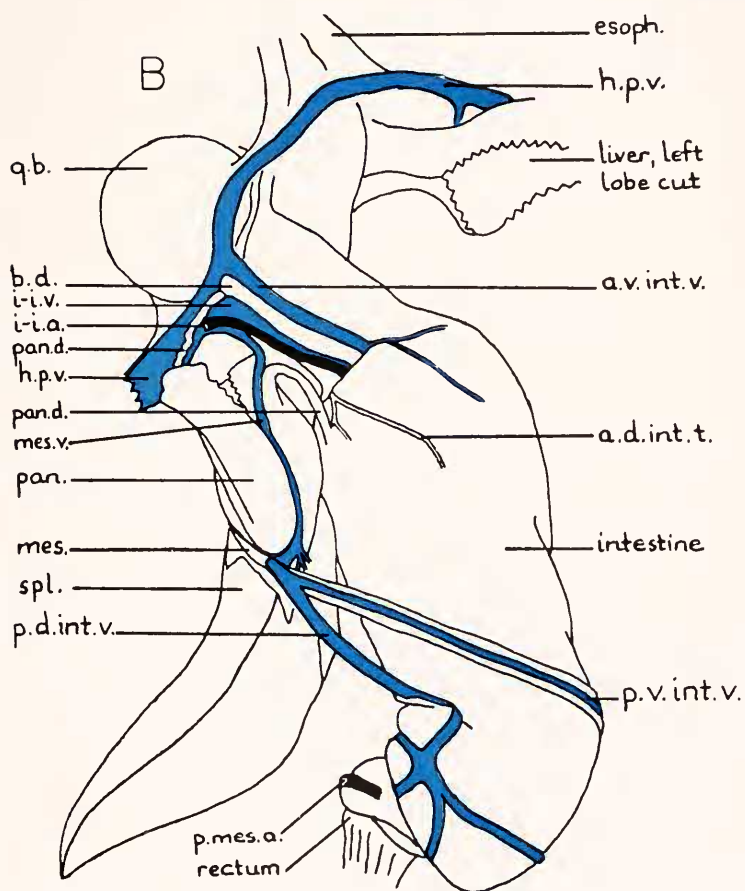
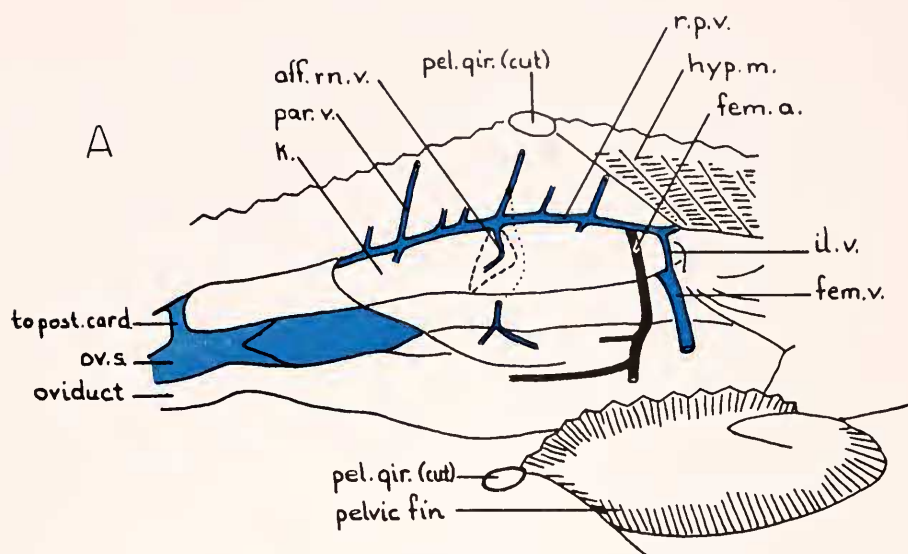


Plate 9. A, Hepatic veins. Lateral view. Right side. $\times 1$. B, Hepatic veins. Lateral view. Left side. $\times 1$. *br.s.*, Brachial sinus; *epid.*, epididymis; *fen.mem.*, fenestrated membrane; *g.b.*, gall bladder; *h.p.v.*, hepatic portal vein; *h.v.*, hepatic vein; *L.gl.*, Leydig's gland; *mes.*, mesentery; *pect.gir.*, pectoral girdle; *post.card.*, posterior cardinal sinus; *sem.ves.*, seminal vesicle; *test.a.*, testicular artery; *t.s.*, transverse septum; *v.d.*, vas deferens.

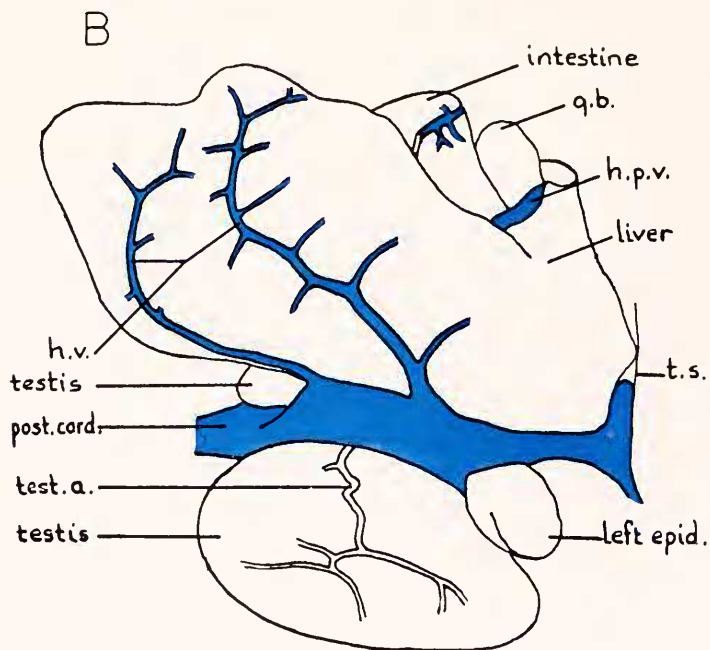
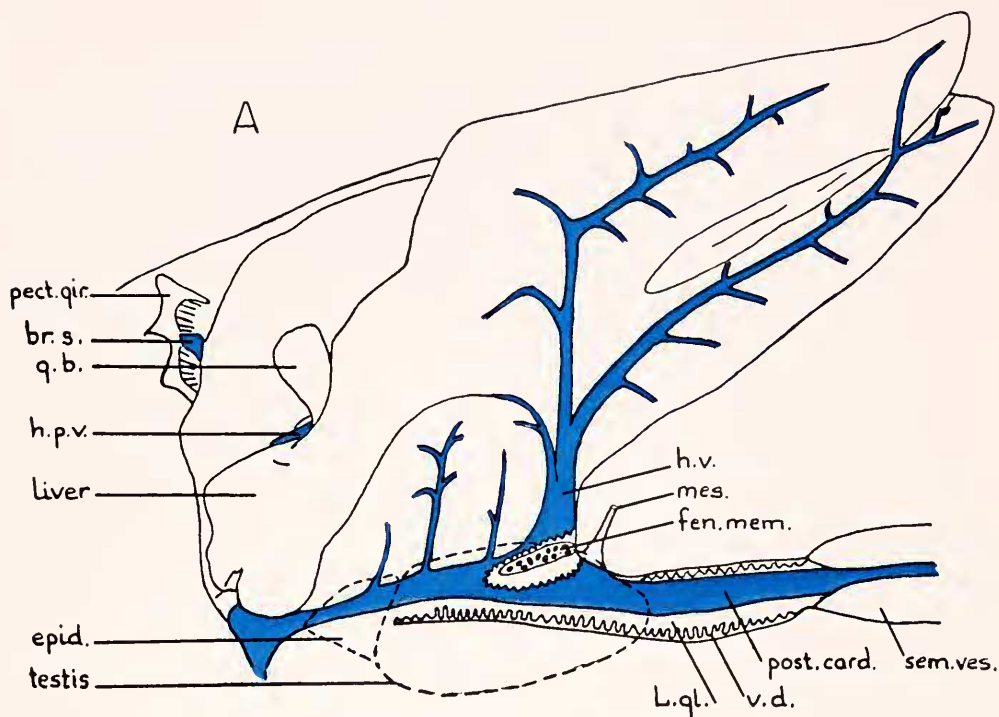


Plate 10. A, The hepatic portal system: veins draining the intestine. $\times 1$. B, The hepatic portal system: veins draining the pancreas and the spleen. $\times 1$. *a.d.int.t.*, Anterior dorsal intestinal tributary; *aux.spl.v.*, auxiliary splenic vein; *a.v.int.v.*, anterior ventral intestinal vein; *b.d.*, bile duct; *cael.a.*, coeliac artery; *esoph.*, esophagus; *g.b.*, gall bladder; *h.a.*, hepatic artery; *h.p.v.*, hepatic portal vein; *i-i.a.*, intra-intestinal artery; *i-i.v.*, intra-intestinal vein; *l-p.v.*, lieno-pancreatic vein; *mes.v.*, mesenteric vein; *pan.*, pancreas; *pan.d.*, pancreatic duct; *pan.v.*, pancreatic vein; *p.d.int.v.*, posterior dorsal intestinal vein; *p.mes.a.*, posterior mesenteric artery; *p-s.a.*, pancreatico-splenic artery; *p.v.int.v.*, posterior ventral intestinal vein; *spl.*, spleen; *spl.v.*, splenic vein.

